

THE BASES OF ANGIOSPERM PHYLOGENY: VEGETATIVE ANATOMY¹

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ABSTRACT

The principal characters of vegetative anatomy which are of phylogenetic significance at the higher levels in angiosperm systematics are defined and discussed in relation to their taxonomic distribution in the Takhtajan and the Cronquist systems of angiosperm classification. In absence of a complete fossil record, application of the phylogenetic method of association, correlation, and common ground plan are illustrated from anatomical data. Vegetative structure contains a wealth of potentially significant systematic information. However, only the evolutionary trends in the secondary xylem and the phylogenetic conclusions that have resulted from recognizing these trends, provide a firm basis of angiosperm phylogeny. In order for the phylogenetic significance of other vegetative anatomical characters to be fully realized, more comprehensive studies must be undertaken and new methodologies and approaches applied. For the most part, anatomical data support the phylogenetic conclusions of the Takhtajan and Cronquist systems of angiosperm classification at the higher taxonomic levels. However, the most reliable application of anatomical information remains in statements of negation of close relationship rather than positive assertions of close affinity.

Anatomical characters have been employed for systematic purposes well over a hundred years. C. R. Metcalfe (1968) has stated that anatomy of the vegetative organs of flowering plants can be taxonomically useful in the following ways: (1) The identification of fragmentary material, (2) the preliminary identification of herbarium specimens, and (3) as an aid toward establishing the interrelationships of taxa at and above the species level. It is important, accordingly, to initially make the distinction between general (diagnostic) taxonomic characters that enable a genus or species to be separated and distinguished from other plants, and characters that assist in our understanding the evolutionary relationships of plants. The primary intention of this paper is to identify the techniques and major characters of vegetative anatomy that form a basis of angiosperm phylogeny at the higher taxonomic levels and how these characters relate to the general systems of angiosperm classification recently proposed by Cronquist (1968) and Takhtajan (1969). Characters of potential phylogenetic significance in angiosperms as a whole and the taxonomic distribution of these characters at different levels in the taxonomic hierarchy are treated. Finally, an attempt is made to evaluate the present state of systematic anatomy and consider what contributions vegetative anatomy may be able to provide in the future with regards to angiosperm phylogeny. Unless indicated otherwise, terms are defined in accordance with Esau (1961).

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TECHNIQUE

The discipline of systematic anatomy is fundamentally descriptive, with comparative data usually obtained from material that has been fixed, sectioned, and stained for microscopical examination and subsequently placed in a reference slide collection. However, temporary preparations of petioles and nodes using freehand procedures can yield rapid data with satisfactory results. Quantitative methods (i.e., statistical correlations) have proven most applicable to the secondary xylem and were the principal tools used in elucidating the major trends of evolution in this tissue. It is manifest that any consideration of the geologic histories of plants should rely heavily on the fossil record. To date, only the secondary xylem of fossil angiosperms has revealed significant phylogenetic information, although, as seen elsewhere in this volume, the fossil record is becoming more useful in regards to other plant structure. Ontogenetic evidence has been employed on occasion and is becoming increasingly valuable.

In recent years, the assumption that a single sample of an organ or tissue provides reliable data upon which to base anatomical generalizations has been shown to be invalid. It is essential, therefore, that the ranges of variability of anatomical characters within the same individual and different individuals in relation to the environment, location of tissues within the plant, and ontogeny be thoroughly investigated. Admittedly, it is often impossible for the comparative anatomist to obtain adequate materials for such studies. However, the goal of all anatomical research should be to make each investigation as comprehensive as possible, and in this vein, Carlquist (1961) has stressed the need to describe the entire range of character variation, or "complement," of a given tissue or structure. A major difficulty the comparative anatomist confronts is distinguishing characters of diagnostic, phylogenetic, and ecological significance. At our present state of knowledge, it is often not possible to separate evolutionary advancement for ecological modification.

The selection of material for study is very critical. It is known, for example, that the first-formed secondary xylem may differ histologically from later-formed wood and thus the uniform selection of mature samples for comparative purposes is desirable. Unfortunately, a large amount of wood data in Solereder's (1908) book were derived from young twigs. Another shortcoming of much early systematic anatomical work was the lack of concern for voucher specimens. It is of utmost importance that the specimens investigated be correctly identified or at least available for taxonomic scrutiny. Without documenting specimens, the value of the anatomical method is considerably reduced. The role of wood collections as bases for research in plant systematics and evolution has been reviewed by Stern (1973) and Wetmore et al. (1974).

In a discussion of phylogeny the terms primitive and advanced with respect to different character states cannot be avoided. Sporne (1948) used the term "primitive character" to mean one which is possessed by a present day taxon and was also possessed by its ancestors. An "advanced character," on the other hand, is one possessed by a present day taxon and not possessed by its ancestor, that is, it replaced an ancestral character during evolution. A fundamental problem confronted by comparative anatomists involved in phylogenetic pursuits is to

determine the direction in which structural modifications have occurred or are occurring, i.e., to identify primitive and advanced characters within the taxonomic units under study, and to determine whether this direction has reversed (Cheadle & Tucker, 1961). Because the erratic fossil record is of little assistance in this regard, other approaches must be employed (see Sporne, 1956). The most successful methods as related to comparative anatomy are termed by Sporne (1956) the doctrines of association, correlation, and common ground plan. Examples of the application of these methods are presented throughout this paper.

That vessel elements evolved from tracheids is certain. Advantageously, the sequence involves characters that are measurable, and, therefore, can be dealt with statistically. Bailey & Tupper (1918) provided the earliest systematic evidence for this trend in a comparison of length of tracheary elements of vascular cryptogams, gymnosperms, and angiosperms. Frost (1930a, 1930b, 1931) extended this work and initiated a detailed statistical analysis of specialization of the secondary xylem in dicots. Frost made two basic assumptions that could be proved by subsequent tests of association and correlation. The first was that the primitive state of the derived structure will resemble the ancestral structure if it can be determined from which structure the other evolved. Since it was assumed that vessel elements evolved from tracheids, Frost deduced that the most primitive vessel elements were those which most resembled tracheids (doctrine of association). If this were not true, then the assumption of a direct relationship is incorrect, or the structures are so widely separated in the evolutionary scale that the tracheid-like condition of the vessel element has been lost. The doctrine of association has been criticized because of assumptions that are made prior to its application. Frost's second assumption, the doctrine of correlation, takes advantage of the fact that primitive characters are frequently associated with other primitive characters. Thus, if one character can be demonstrated to be primitive (e.g., scalariform perforation plates on the vessel end wall), then characters correlated with this feature are probably also primitive. The doctrine of the common ground plan assumes that any character present in all individuals of a taxon, or the most common character state among a group of related plants, must be the ancestral or primitive state.

Phylogenetic speculation involving the concepts of tissue conservatism, recapitulation of phylogeny during ontogeny, and teratology generally have met with criticism and limited success.

MAJOR REFERENCE WORKS

Systematic anatomy had its beginnings in the middle 1800's with the contributions of Sanio, Radlkofer, Vesque and others. Application of the anatomical method toward the solution of systematic problems was strongly advocated by Fritsch (1903) and thoroughly reviewed by Metcalfe (1946, 1953, 1954, 1959, 1961), whose thoughts have been freely drawn upon in the preparation of this paper. The first comprehensive, systematic summary of anatomical information was provided by Hans Solereder whose *Systematic Anatomy of the Dicotyledons* (2 vols.) was published in English translation in 1908. These landmark volumes provided the basis of all subsequent work on comparative vegetative anatomy

and are still indispensable reference sources. In 1950 a monumental two volume work *Anatomy of the Dicotyledons*, by C. R. Metcalfe and L. Chalk appeared, again dealing with aspects of vegetative anatomy, although emphasizing wood structure as a systematic and phylogenetic tool. The authors' objectives were "... to write this book in the hope that a modern counterpart to Solereder's well-known treatise on the same subject would lead towards a more natural classification of the Dicotyledons and make some contributions to our knowledge of phylogeny." Interestingly, as late as 1950, our knowledge of dicotyledonous vegetative anatomy could still be contained in only two volumes. Work is currently underway in the Jodrell Laboratory at Kew on a revision of this book.

Reference sources on the anatomy of monocotyledons begin with Solereder and Meyer's never completed *Systematische Anatomie der Monokotyledonen* published between 1928 and 1933. Quite recently, a series dealing exclusively with vegetative anatomy entitled *Anatomy of the Monocotyledons* has begun to appear under the editorship of C. R. Metcalfe. The subjects, authors, and dates of publication of completed books are as follows: Vol. I, Gramineae by C. R. Metcalfe (1960); Vol. II, Palmae by P. B. Tomlinson (1961); Vol. III, Comelinales-Zingiberales by P. B. Tomlinson (1969); Vol. IV, Juncales by D. F. Cutler (1969); Vol. V, Cyperaceae by C. R. Metcalfe (1971); and Vol. VI, Dioscoreales by E. S. Ayensu (1971).

Also worthy of mention as a reference source is the *Handbuch der Pflanzen-anatomie* that was edited in the first edition by K. Linsbauer and is now being published in the second edition as the *Encyclopedia of Plant Anatomy*. Careful attention should also be given to *Comparative Plant Anatomy* by Carlquist (1961).

PRINCIPAL CHARACTERS OF PHYLOGENETIC SIGNIFICANCE

SECONDARY XYLEM

During the past fifty years the value of wood anatomy, and vessel element evolution in particular, in the study of the phylogeny and classification of angiosperms has been clearly established. In no other vegetative tissues of the plant are the trends of evolution as clearly defined. These trends were recognized entirely without reference to existing taxonomic systems and thus without reference to the relative primitiveness or advancement of the plants in which they occur. The many achievements of wood anatomy in this respect have been subjects of several reviews (Chalk, 1937, 1944; Tippe, 1946; Vestal, 1940; Carlquist, 1961) and have perhaps tended to present vegetative anatomy in a rather one-sided manner. Bailey (1951) and Metcalfe (1954), among others, have noted that a phenetic classification of the dicotyledons, reflecting levels of evolutionary advancement, could be constructed entirely from anatomical information. Such a classification would be extremely difficult, if not impossible, to construct if vegetative characters exclusive of wood were considered. The vast amount of comparative data on wood structure results in part from the economic importance of wood, the relative ease of specimen preparation, and the fact that secondary xylem is often well preserved in herbarium specimens and fossil materials as a result of rigid cell walls. Major wood characters of proven phylogenetic value

are outlined and discussed below. Terms are defined in accordance with the *Multilingual Glossary of Terms Used in Wood Anatomy* (Committee on Nomenclature, 1964).

I. Tracheids and fibers (imperforate tracheary elements).

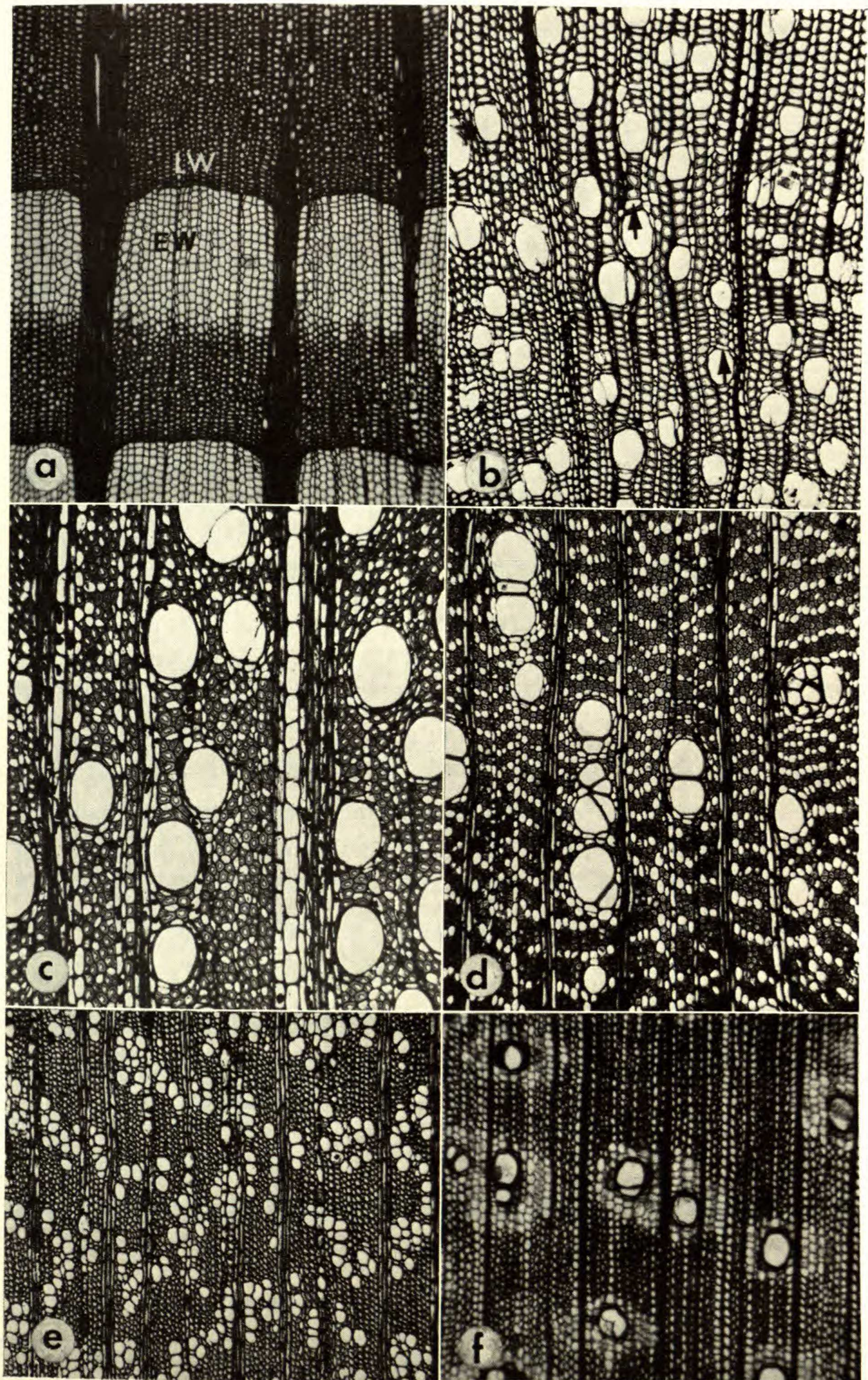
A. Types.

1. Tracheid. An imperforate wood cell with bordered pits to congeneric elements (Figs. 3e-f).
2. Vascentric tracheid. A short, irregularly-formed tracheid in the immediate proximity of a vessel and not forming part of a definite axial row (Fig. 3p).
3. Fiber. A general term of convenience in wood anatomy for any long, narrow cell of wood or bast other than vessels and parenchyma. Note: often further qualified as wood fibers or bast fibers; the former including both the tracheids of gymnosperms and libriform wood fibers and fiber-tracheids of wood angiosperms. Also used loosely for wood elements in general.
4. Fiber-tracheid. A fiber-like tracheid; commonly thick-walled with a small lumen, pointed ends, and bordered pit pairs having lenticular to slit-like apertures. This term is applicable to the late wood tracheids of gymnosperms as well as to the fiber-like tracheids of woody angiosperms (Figs. 3b-d).
5. Libriform wood fiber. An elongated, commonly thick-walled cell with simple pits; usually distinctly longer than the cambial initial as inferred from the length of vessel members and parenchyma strands (Fig. 3a).
6. Septate wood fiber. A fiber with thin transverse walls across the lumen (Fig. 3o).

B. Wall thickness, sculpture, and cell length. Wall thickness ranges between very thin (lumen much greater than thickness of wall) and very thick (lumen almost completely closed). Element length ranges between very short (up to 1000 μm) and very long (over 2000 μm). Elements may have spiral thickenings that are helical ridges on the inner face of, and part of, the secondary wall.

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FIGURE 1. Transverse sections of dicotyledonous woods.—a. *Trochodendron aralioides* (Trochodendraceae), a primitively vesselless angiosperm showing the secondary xylem composed of tracheids. Distinction can be noted between tracheids of the late-wood (LW) and early-wood (EW); $\times 46$.—b. *Schumacheria castaneifolia* (Dilleniaceae). This wood shows solitary, angular vessels and mostly scanty axial parenchyma (arrows). The imperforate tracheary elements are fiber tracheids; $\times 55$.—c. *Dillenia pentagyna* (Dilleniaceae). Although this wood still has a comparatively primitive structure, the vessels are more rounded in outline and the axial parenchyma is both paratracheal scanty and apotracheal diffuse to diffuse-in-aggregates; $\times 55$.—d. *Scytopetalum tieghemii* (Scytopetalaceae). In this wood the vessels are distributed as solitary pores and pore multiples. Imperforate tracheary elements are thick-walled libriform fibers and axial parenchyma is mostly diffuse-in-aggregates; $\times 55$.—e. *Pittosporum tenuifolium* (Pittosporaceae). Note the pores are distributed in pore chains and radial pore multiples; $\times 55$.—f. *Paulownia tomentosa* (Scrophulariaceae). Note the vascentric parenchyma; $\times 46$.



- II. Vessels (perforate tracheary elements). A vessel is an axial series of cells (vessel members or elements) that have coalesced to form an articulated tube-like structure of indeterminate length; the pits to congeneric elements are bordered.
- A. Pore (vessel) distribution.
1. Solitary pores. A pore completely surrounded by other elements (Figs. 1b-c).
 2. Pore chain. A series or line of adjacent solitary pores (Fig. 1e).
 3. Pore multiple. A group of two or more pores crowded together and flattened along the lines of contact so as to appear as subdivisions of a single pore. The most common type is a radial pore multiple, in which the pores are in radial files with flattened tangential walls between them (Fig. 1d). Another type is a pore cluster, in which the grouping is irregular.
- B. Vessel element shape, wall thickness, and size. Vessel outline as seen in transverse section ranges from angular (Fig. 1b) to circular (Fig. 1d), with variation from thin to thick walled. Pore diameter as measured in transverse section ranges between extremely small (up to 25 μm) to extremely large (over 400 μm). Length of vessel elements as recorded from tip to tip range from extremely short (less than 175 μm) to extremely long (over 1900 μm).
- C. Perforation plates. A perforation plate is a term of convenience for the area of the wall (originally imperforate) involved in the coalescence of two members of a vessel. Principal types of perforation plates are scalariform and simple. A scalariform plate has multiple perforations elongated and parallel (Fig. 3g). The remnants of the plate between the openings are called bars. Significant variations include the number of bars and whether the perforations are completely bordered (Fig. 3g), bordered to the middle, bordered at the ends (Fig. 3h), or non-bordered. A simple perforation plate consists of a single and usually large and more or less rounded opening in the perforation plate (Fig. 3k). Perforation plate end walls range from highly oblique to transverse (Figs. 3g-k).
- D. Intervascular pitting. A term used (a) in a wide sense for pitting between tracheary elements, and (b) in a narrower sense in wood anatomy for pitting between vessel members.
1. Scalariform. Pitting in which elongated or linear pits are arranged in a ladder-like series (Fig. 3g).
 2. Opposite. Multiseriate pitting in which the pits are in horizontal pairs or in short horizontal rows (Figs. 3h-i). Note: when pits are crowded, the outlines of the borders tend to become rectangular in surface view.
 3. Alternate. Multiseriate pitting in which the pits are in diagonal rows (Figs. 3j-k).
- III. Rays. A ray is a ribbon-like aggregate of cells extending radially in the xylem and phloem. Xylem rays are classified on the basis of type and size.

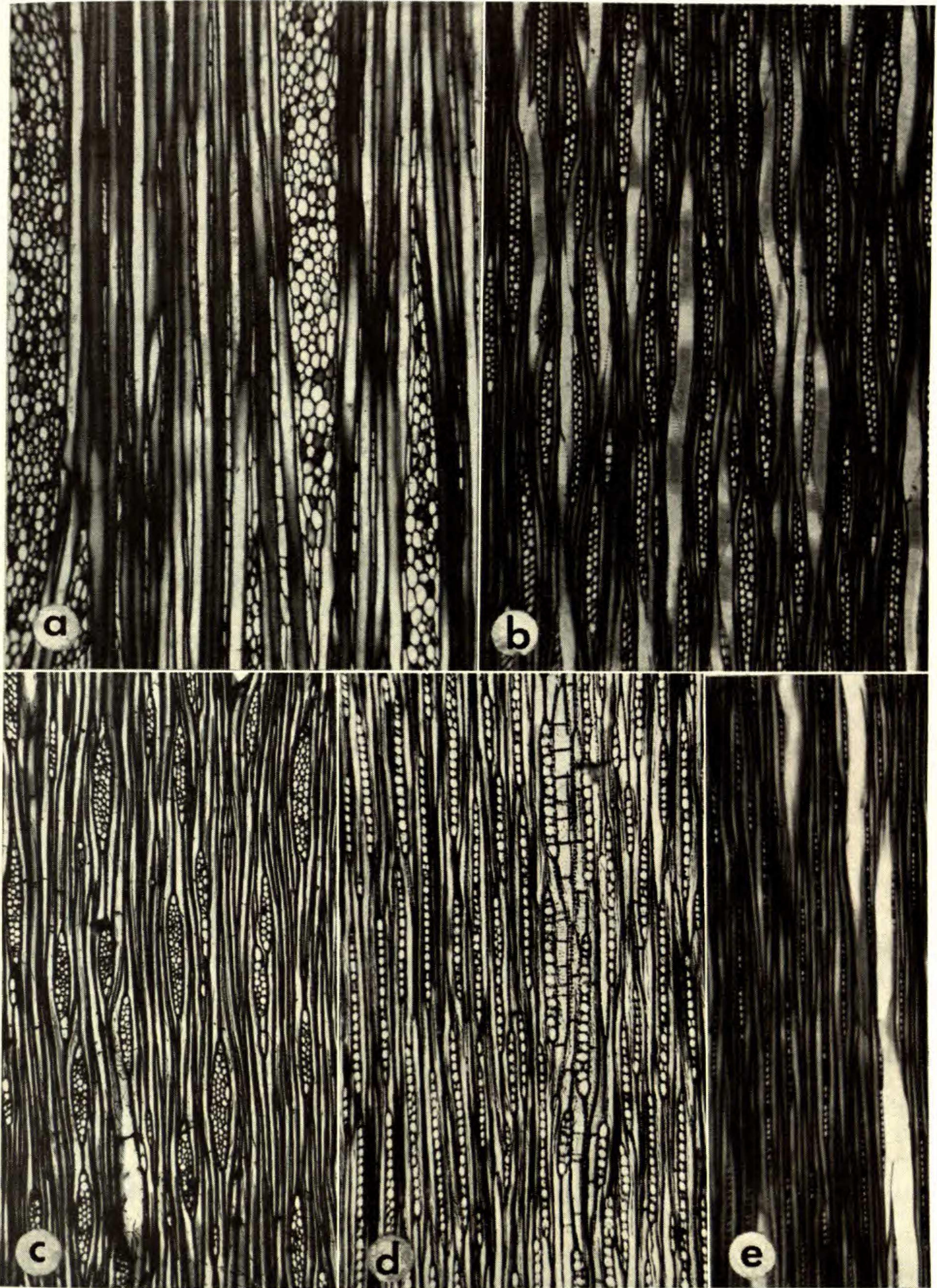
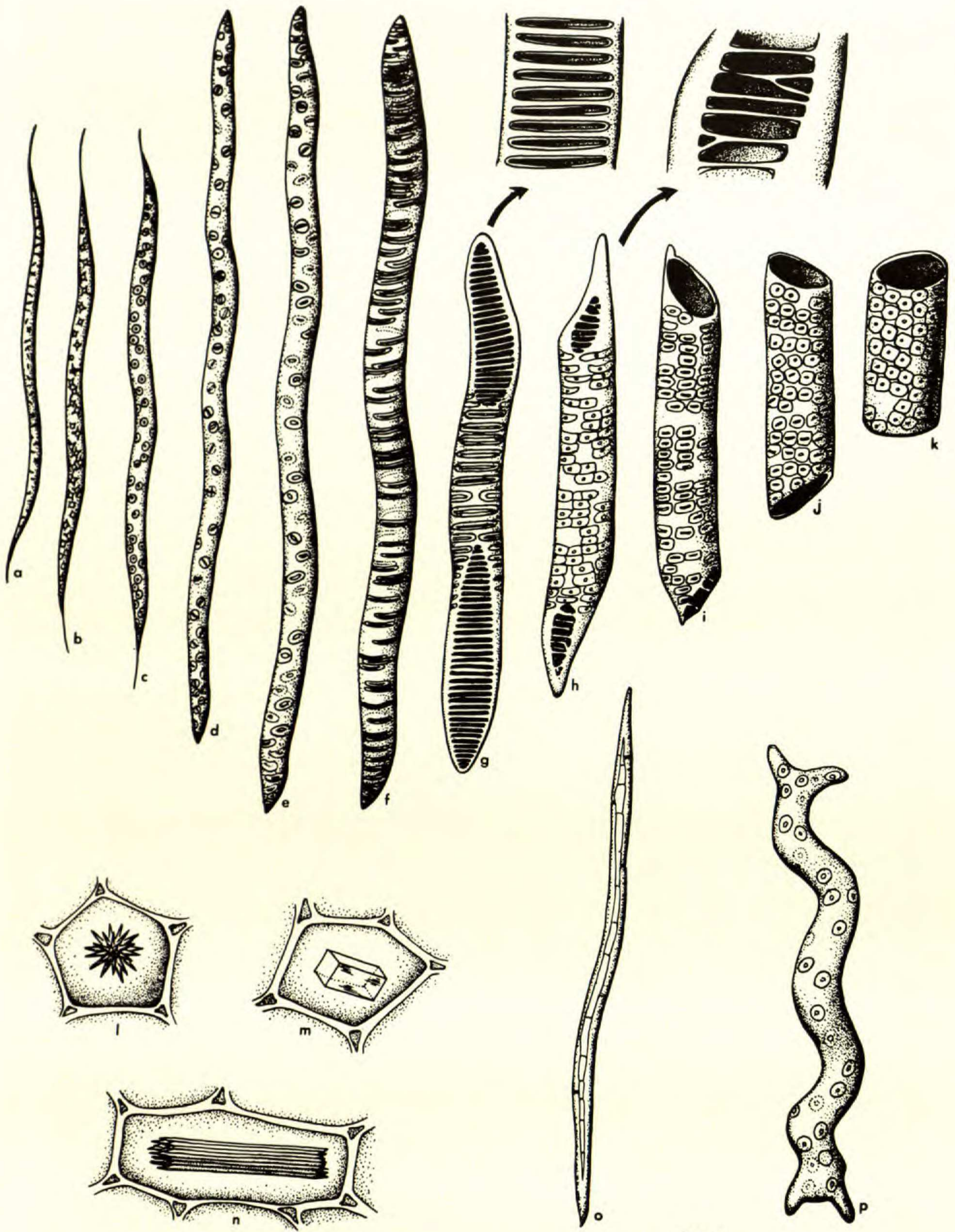


FIGURE 2. Tangential sections of dicotyledonous woods.—a. *Bubbia semecarpoides* (Winteraceae). Note primitive ray histology in this wood. Both heterocellular multiseriate and uniseriate rays are present; $\times 46$.—b. *Magnolia grandiflora* (Magnoliaceae). This wood shows both uniseriate and multiseriate (biseriate) heterocellular rays. The uniseriate wings on the multiseriate rays are often reduced to a single cell; $\times 46$.—c. *Pittosporum kauaiense* (Pittosporaceae). Rays are heterocellular with multiseriate body of the rays composed predominately of procumbent cells; $\times 55$.—d. *Gonystylus warburgianus* (Thymelaeaceae). The rays of this species are predominately uniseriate and nearly homocellular; $\times 55$.—e. *Populus deltoides* (Salicaceae). Note the exclusively uniseriate and homocellular rays; $\times 46$.



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FIGURE 3. Cell types of the secondary xylem.—a-d. Wood fibers.—a. Libriform wood fiber. Note the simple pit and pointed ends of this most advanced of wood fiber types.—b-d. Fiber-tracheids. Note the progressive loss of the pit border from d to b.—e-f. Tracheids. The cell figured in e has circular-bordered pits whereas the element pictured in f has scalariform pits.—g-k. Vessel elements.—g. The cell pictured here represents a primitive vessel element type with many-barred scalariform perforation plates that are fully bordered (inset) and scalariform intervascular pitting.—h. This cell also has scalariform perforation plates but the number of bars is reduced in number and they are bordered only at the ends (inset). The intervascular pitting is multiseriate and arranged in an opposite manner.—i. This vessel element represents an

With respect to type, rays are heterocellular and homocellular. A heterocellular ray is one in which the individual rays are composed of both procumbent cells and square or upright cells (Figs. 2a–c), whereas a homocellular ray is composed wholly of cells of the same morphological type, i.e., all procumbent or all square or upright (Fig. 2e). With respect to size, rays are described as uniseriate if they are one cell wide as seen in tangential section (Figs. 2d–e), and multiseriate if they are more than one cell wide (Figs. 2a–c). Ray height is generally recorded in terms of the number of cells.

- IV. Axial parenchyma. Parenchyma cells derived from fusiform cambial initials. Axial parenchyma distribution (as seen in transverse section) is classified in the following way.
- A. Apotracheal parenchyma. Axial parenchyma typically independent of the pores or vessels.
1. Terminal parenchyma. Apotracheal parenchyma cells occurring either singly or forming a more or less continuous layer of variable width at the close of a season's growth.
 2. Diffuse parenchyma. Single apotracheal parenchyma strands or cells distributed irregularly among fibers (Fig. 1c).
 3. Diffuse-in-aggregates. Apotracheal parenchyma cells that tend to be grouped in short tangential lines from ray to ray (Figs. 1c–d).
 4. Banded apotracheal parenchyma. Axial parenchyma forming concentric lines or bands. Note: termed apotracheal banded, if typically independent of the vessels; paratracheal banded, if associated with the vessels.
- B. Paratracheal parenchyma. Axial parenchyma associated with the vessels or vascular tracheids.
1. Scanty parenchyma. Incomplete sheaths or occasional parenchyma cells around the vessels (Figs. 1b–c).
 2. Vascentric parenchyma. Paratracheal parenchyma forming a complete sheath around a vessel, of variable width and circular or slightly oval in cross section (Fig. 1f).
 3. Aliform parenchyma. Paratracheal parenchyma with wing-like lateral extensions, as seen in cross section.
 4. Confluent parenchyma. Coalesced aliform parenchyma forming irregular tangential or diagonal bands, as seen in cross section.

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intermediate stage in evolution with a scalariform perforation plate at one end and a simple perforation plate at the other end. Intervascular pitting is still essentially opposite.—j. The cell pictured here is further advanced as evidenced by the exclusively simple perforation plates that are tending to become transverse in orientation. The intervascular pitting is best described as transitional between opposite and alternate.—k. This vessel element is the most advanced type illustrated, with simple, transverse perforation plates and alternate intervacular pitting. Also note its short length and increase in width.—l–n. Crystal types.—l. Druse.—m. Prismatic form.—n. Raphides.—o. Septate libriform wood fiber.—p. Vascentric tracheid. Note the irregular shape of this element. (From A. E. Radford, W. C. Dickison, J. R. Massey & C. R. Bell. *Vascular Plant Systematics*. Copyright 1974 by Harper & Row, Publ. Used with permission.)

The trends of evolution of the vessel element have been firmly established through extensive and intensive comparative anatomical studies on both fossil and living material, statistical analyses (i.e., measurements and correlations), and ontogenetic studies. Therefore, the evolutionary trend from tracheids to vessel elements is the most reliable tool known in the study of phylogeny. This is true because this trend is both largely unidirectional and irreversible.

It has been shown that angiosperm vessel elements (in secondary wood) have been phylogenetically derived from scalariform-pitted tracheids by the loss of pit membranes in the regions of tracheid overlap. Therefore, vessel elements which are most tracheid-like, viz., elongate, narrow, many scalariform perforations in the end walls, etc., are the most primitive type. Other known major trends of vessel element specialization (Figs. 3g-k) are: (1) change in perforation plates from scalariform, many barred, and fully bordered, to few barred and borders absent, to more advanced porous oblique and transverse porous plates; (2) angle of end wall highly oblique and tapering (much overlap) to transverse; (3) reduction in vessel element length; (4) change in appearance in transverse section from angular to circular; (5) increase in pore diameter; (6) change in intervacular pitting from scalariform and bordered to opposite and alternate multiseriate; and (7) change in vessel distribution from solitary to extensive aggregate groupings of vessels. Cox (1948a, 1948b) and Adams (1949) used the ratio of average vessel element length to average vessel element diameter as an index of advancement. A relatively primitive condition is expressed by a high ratio, a relatively advanced condition by a low ratio. Concomitant with changes in vessel elements are modifications in the fusiform cells of the vascular cambium from long initials with overlapping ends that divide in a pseudo-transverse manner to advanced initials that are reduced in length, and undergo radio-longitudinal division.

Although the above trends of vessel evolution are believed to be firmly established, Beck (1970) has pointed out the appearance by Middle Devonian time of circular bordered pits in either primary or secondary xylem of coniferophytic progymnosperms and primitive pteridosperms. In his opinion the acceptance of the scalariform bordered pit as primitive in seed plants should be reconsidered. To quote Beck, "In view of the early appearance of the circular bordered pit in the progymnosperms and the preponderant occurrence of this type in the secondary xylem of cycadophytic and coniferophytic gymnosperms, it seems not unreasonable to suggest that the circular bordered pit might be the basic, primitive type in the gymnosperm-angiosperm line of evolution. This is not to say, necessarily, that the circular bordered pits of some angiosperms might not have evolved from the scalariform pits of their ancestors, whether gymnosperm or angiosperm. In these groups this might be interpreted to have been accomplished through neoteny. The circular bordered pits of other groups of angiosperms might simply reflect their ancestry from gymnosperms with circular bordered pits." Furthermore, Baas (1974) and van der Graaff & Baas (1974) have made some very interesting correlations between wood structure and environmental factors. Studies of xylem of 24 dicotyledonous genera, with *Ilex* being the most thoroughly investigated, established that there has occurred a

strong shortening of vessel elements with increasing latitude and altitude. This presumably very important climatic influence on vessel element length (the number of bars per scalariform perforation plate is unaffected) led these workers to the belief that the general phylogenetic trend from long to short vessel elements "must be reversible to a considerable extent" (Baas & van der Graaff, 1974). Their data also suggests that climatic changes have led to other directing influences on wood specialization.

Other well known major phylogenetic trends in the secondary xylem, as revealed by statistically significant correlations using features of vessel elements, include the evolution from tracheids to fiber-tracheids to advanced libriform fibers through a progressive increase in cell length (as compared to vessel elements) with a concomitant reduction in pit size and number and eventual elimination of the tracheid pit border (Figs. 3f-a). Primitive woods have both uniseriate and multiseriate rays that are heterocellular and high-celled; the multiseriate rays have long uniseriate wings (Fig. 2a). Specialization results in the reduction and loss of either the multiseriate or uniseriate rays (or both), the rays becoming homocellular (Fig. 2e) and reduced in height with the uniseriate wings of multiseriate rays reduced to a single cell (Figs. 2b-c). The condition of stratified rays formed by a storied cambium is an extreme advancement. Apotracheal diffuse axial parenchyma is regarded as the primitive state from which more advanced paratracheal types (vasicentric, aliform, confluent) were derived; however, Bailey (1957) points out that the available data do ". . . not provide a thoroughly reliable basis for arranging the diversified patterns in a single linear series of increasing structural specialization." The phylogenetic significance of the absence of wood parenchyma is unclear.

Additional features of wood structure are believed to represent sporadically occurring divergent trends of specialization whose presence in woods does not imply a close genetic relationship. These include helical thickenings on the walls of tracheary elements and fibers, imperforate tracheary elements which become septate or retain a living protoplast, formation of vascular tracheids and vasicentric tracheids, excessive thickening of walls and widening of vessel element diameter (as in lianas), various reticulate perforation plates or other modifications of perforation plates, and extensive aggregations of vessels in diversified patterns (Bailey, 1957). Furthermore, Carlquist (1962) has shown that primitive features of the primary xylem may occasionally be extended into the secondary xylem (paedomorphosis or juvenilism) in plants that are otherwise specialized. This theory of paedomorphosis has recently been challenged by Mabberley (1974).

The great value of wood anatomy as a guide to understanding angiosperm evolution lies not only in the fact that trends toward specialization are well defined, but that all stages in evolutionary specialization are observable in extant angiosperms. Therefore, there is not the slightest doubt that the absence of vessels (Fig. 1a) in eleven genera of woody dicotyledons represents the retention of a primitive feature. The largest number of vesselless genera (7) occur in the Winteraceae, whereas the Trochodendraceae, Tetracentraceae, Amborellaceae,

and Chloranthaceae contain a single vesselless genus each. However, based on the sole evidence of lack of vessels, these genera are not necessarily the most primitive angiosperms, since evolution proceeds independently in all organs and tissues of plants. The absence of vessels in plants belonging to families like Cactaceae is clearly the result of extreme specialization (Bailey, 1966). The importance of how plant habit and the factors of the environment and ecology affect wood structure and the trends of xylem evolution has been emphasized recently by Carlquist (1966, 1969a, 1969b). To date, the single most important guiding principle regarding wood anatomy and phylogeny (Bailey, 1944) emphasizes the impossibility (unlikelihood) that a taxon with specialized xylem gave rise directly to a taxon with less specialized xylem. Accordingly, wood anatomy is more useful in negations than assertions of positive relationship.

Other features of the secondary xylem are diagnostic in so far as they are restricted to certain families or genera; however, their phylogenetic significance remains dubious. Distinctive tile ray cells are confined to certain genera of the Bombacaceae, Sterculiaceae, and Tiliaceae, whereas upright sheath cells located on the margins of multiseriate rays are of comparatively widespread occurrence. Vestured pits are reported for 24 families of dicotyledons (Bailey, 1933), with a concentration in the Myrtales. Solitary prismatic crystals (Fig. 3m) are relatively widespread, although such forms as raphides (Fig. 3n), druses (Fig. 3l), and crystal sand have a more restricted distribution, and, therefore, are of greater taxonomic interest (Metcalf & Chalk, 1950).

The relationship of wood anatomy to proposed phylogenetic relationships of the Cronquist and Takhtajan systems of angiosperm classification is presented below, along with examples illustrating the phylogenetic application of wood data at the level of orders within a given subclass, families within an order, and character correlation within a single family. Results presented by Chalk (1937) following an anatomical survey of 1,272 genera of dicotyledons in relation to the general systems of Bentham and Hooker, Engler, and Hutchinson are instructive. Utilizing four degrees of wood specialization—scalariform perforation plates, fiber-tracheids, libriform fibers, and storied structure—Chalk found both primitive and advanced characters widely distributed among Engler's orders. These data indicate that whereas individual families and genera tend to be anatomically homogeneous, orders and categories of higher rank tend to be comparatively anatomically heterogeneous (Metcalf, 1954). It is not surprising, therefore, to find that the Cronquist and Takhtajan subclasses, which are morphologically ill-defined, are also anatomically extremely heterogeneous. The 110 families listed by Metcalf & Chalk (1950) as containing genera with scalariform perforation plates are widely distributed throughout the subclasses, although scalariform plates occur exclusively in some families and very infrequently in others. Only the Centrospermae (Caryophyllidae), which contains few woody members, tends to be anatomically more or less homogeneous (Metcalf, 1954).

The subclass Magnoliidae with a preponderance of primitive characters has much to recommend it as the basal group. Although ordinal concepts differ, concentrated within the Magnolialian-Lauralian assemblages are the vesselless Winteraceae and Amborellaceae, as well as the following families whose genera

possess exclusively scalariform perforation plates: Eupomatiaceae, Austrobaileya-ceae, Canellaceae, Degeneriaceae, Trimeniaceae, Gomortegaceae, and Illiciaceae (Ranunculidae of Takhtajan). The vesselless species *Sarcandra irvingbaileyi* (Chloranthaceae) is placed in the Piperales by Cronquist and in the Laurales by Takhtajan. Magnolialian families containing vessels with both scalariform and simple perforation plates include Magnoliaceae (simple plates in temperate species only), Himantandraceae, Myristicaceae, Lauraceae, and Monimiaceae. Rather advanced xylem, as evidenced by the occurrence of exclusively simple perforation plates, characterizes Annonaceae, Calycanthaceae, Hernandiaceae (and Gyrocarpaceae), and Lactoridaceae, although in the latter family, the extremely specialized wood is related to growth habit (Carlquist, 1964). Similar habit-related specialized xylem occurs in members of the Schisandraceae. Correlated with the absence of vessels or presence of primitive vessel elements are heterocellular rays, fiber-tracheids, and diffuse or scanty parenchyma.

The diversity of wood anatomy in the Hamamelididae is enormous, ranging from the vesselless Trochodendrales to moderately advanced and advanced families in the Urticales and Leitneriales. The absence of vessels in the Trochodendrales, among other characters, undoubtedly makes this the primitive order. Both Cercidiphyllaceae and Eupteleaceae have vessels with exclusively scalariform perforation plates. Although the Trochodendrales could only have been derived from a vesselless ancestry (from either an extinct or extant group), wood anatomy does not provide positive evidence that the porous genera of the Hamamelididae were derived directly from the Trochodendrales. Along with other wood features, the occurrence of few-barred scalariform perforation plates in a few members of the Ulmaceae, and their corresponding absence in other families, supports the primitive position of the Ulmaceae in the Urticales (Sweitzer, 1971).

Subclasses Dilleniidae and Rosidae are both regarded as derived from the Magnoliidae (within or near the Magnoliales). Wood anatomy is consistent with this conclusion and indicates a derivation from only the most unspecialized members of the magnolialian complex. Although there are no vesselless woods in these two large subclasses, various genera are at a very low level of anatomical advancement. In the Dilleniidae, exceedingly primitive vessel elements (exceeding 2000 μm in length and with over 100 scalariform bars) are found in the Dilleniaceae, Theaceae, and the genus *Saurauia*, with only slightly more advanced elements in other members of the Ericales. In the Rosidae, nearly the total range of variability is present in the basal order Rosales which encompasses the comparatively primitive Eucryphiaceae and Cunoniaceae and the advanced Leguminosae. The need for harmonizing wood anatomy with other systematic evidence is illustrated by the Cornales where wood structure indicates a lower evolutionary level.

As regards the largely herbaceous Asteridae, a high level of xylem evolution is correlated with advanced floral characters. Simple perforation plates predominate, along with other indices of advancement. Members of a few basically herbaceous families (e.g., Campanulaceae, Goodeniaceae) to a limited extent have become secondarily woody in response to highly specific ecological condi-

tions (Carlquist, 1969a, 1969b). Typically, the wood of such plants is unlike that found in fundamentally woody families. Carlquist (1966) describes the wood of Compositae as advanced to highly advanced and notes that it is indistinguishable from woods of other specialized families such as Scrophulariaceae. Because the range of structural variability is so narrow in composites, Carlquist was unable to use major trends of wood evolution for systematic or phylogenetic purposes, but instead had to rely on characters relating to habit, in addition to so-called minor features.

As would be expected, woody anatomy has proven most valuable in intra-familial classification and phylogeny when families exhibit wide ranges of structural variability. A classic example is found in the Icacinaceae where Bailey & Howard (1941a, 1941b, 1941c) were able to recognize successive levels of evolutionary advancement and utilized anatomical data for subdividing the family into subfamilies and tribes. In the Dilleniaceae I was able to support recognition of two subfamilies and correlate wood data with other vegetative and floral evidence, all of which showed that the Old World genera are, as a whole, more primitive than New World taxa (Dickison, 1967, 1970). Furthermore, the dilleniaceous genus *Acrotrema* is of interest from an evolutionary viewpoint because it is a small, nearly herbaceous plant in an otherwise woody family, and it is one of the few dicotyledonous herbs in which the vessel elements possess exclusively scalariform perforations. The structural variability in the secondary xylem of the Violaceae recently enabled Taylor (1972) to substantiate the division of the subfamily *Violoideae* into two tribes. Heimsch & Wetmore (1939) found xylem anatomy to correlate to a large degree with inflorescence morphology in evaluating relationships in the Juglandaceae, although attempts to uncover lines of xylem specialization within genera were not successful. On the other hand, when a family is comparatively uniform anatomically, as is the case in the Connaraceae, the significance of xylem data to intrafamilial classification is considerably lessened (Dickison, 1972).

SECONDARY PHLOEM

Unlike xylem, information on the comparative anatomy and evolutionary trends in phloem is meager (Esau et al., 1953). For example, witness the absence of phloem data in Metcalfe & Chalk (1950). The subject of phloem is thoroughly reviewed in Esau (1969). Suggested trends of specialization relate mostly to sieve elements in secondary phloem of dicotyledons and metaphloem elements of monocotyledons, and have by no means been demonstrated to be unidirectional or irreversible. Composing the secondary phloem are the principal conducting cells, the sieve elements, in combination with various amounts of phloem parenchyma, sclerenchyma, and ray parenchyma. With regard to sieve elements, Cheadle & Whitford (1941) recognized two basic types, the sieve cell and sieve tube element. The sieve cell is interpreted as a less specialized element with relatively undifferentiated sieve areas (i.e., narrow pores and thin connecting strands), and lacking highly developed sieve plates and companion cells. More advanced sieve tube elements have specialized sieve plates on the end walls, have accompanying companion cells, and are superimposed on one another in longitudinal series forming a sieve tube. Sieve plates may be compound, that is,

composed of several highly differentiated sieve areas, or simple, that is, composed of a single sieve area. Also, end walls range in orientation from highly oblique to transverse. Although the distinction between these cell types is not always sharp, gymnosperms and lower vascular plants possess sieve cells whereas angiosperms are characterized by sieve tube elements and associated companion cells.

The sieve cell is generally regarded as the primitive type of conducting element from which the sieve tube element arose. Major trends of sieve tube element specialization (Esau et al., 1953) are believed to involve (1) localization of specialized sieve areas on the end walls, (2) change in orientation of end walls from very oblique to transverse, (3) progressive change from compound to simple sieve plates, and (4) progressive decrease in conspicuousness of the sieve areas on the side walls, although the relation between specialization of lateral sieve areas and the sieve tube element is not consistent (Zahur, 1959). Esau (1969) has stressed that comparative data of lateral sieve areas should come only from walls between contiguous sieve elements. The same general trends have also been agreed upon for monocotyledons (Cheadle, 1948; Cheadle & Whitford, 1941). Measurements of cell length, width, and size of sieve pore area have yet to demonstrate the same phylogenetic significance proposed for tracheary tissue. However, Zahur (1959) is of the opinion that there has been a phylogenetic decrease in sieve tube element length (realizing secondary septation can occur) accompanied by decrease in the length of the end walls and increase in the size of sieve plate pores. Following earlier works, Zahur classified sieve tube elements into three categories of increasing specialization: (I) elements long (400 μm or more), with very oblique sieve plates containing 10 or more sieve areas; (II) elements of medium length, with oblique sieve plates containing 2 to 10 sieve areas; and (III) elements short, with slightly oblique to transverse, simple plates. It is clear that there is rather uniform agreement that the most primitive sieve tube elements are ones that most resemble sieve cells.

Zahur (1959) also classified companion cells into types reflecting ascending evolutionary advancement. Type A are cells that are much shorter than the sieve tube elements and occur singly, usually at the corners; type B are cells as long as the sieve tube element; and Type C are cells that are septate in addition to being as long as the sieve tube element. Zahur found companion cell type to be constant within families, and occasionally orders, with the greatest variability occurring in families whose "naturalness" has been questioned.

Although the evidence is indecisive, Zahur (1959) regarded abundant, extremely variable and irregular parenchyma to be advanced, whereas scanty parenchyma showing little variation in size probably represents a primitive condition because of its association with polypetalous families. He could find no basis for deciding whether the presence or absence of phloem sclerenchyma was structurally primitive or advanced. However, Eames (1961) regarded the presence of phloem fibers as an advanced state.

The distribution of sieve element types in the Magnoliales-Laurales correlates with the concentration of other primitive characters. As far as is known, unspecialized sieve cells occur in only one angiosperm, *Austrobaileya scandens*

(Austrobaileyaceae) (Bailey & Swamy, 1949; Srivastava, 1970). It is reassuring that this genus belongs in the otherwise primitive Magnoliidae, although, why the vascular tissues of this genus have remained at a low level of advancement and have not become specialized in response to the liana habit is unclear. Otherwise in the Magnoliales (sensu Cronquist), Type I sieve tube elements occur in Magnoliaceae, Myristicaceae, Canellaceae, Illiciaceae, and Schisandraceae. Type II elements characterize members of Himantandraceae, Monimiaceae, Calycanthaceae, and Lauraceae. Advanced Type III elements distinguish the Annonaceae, a family also with comparatively advanced wood.

Other unrelated families containing Type I sieve tube elements include Cericidiphyllaceae, Passifloraceae, Rosaceae (in part), Myrtaceae, Cunoniaceae, Icacinaceae, Pittosporaceae, Araliaceae, Rutaceae (in part), and Euphorbiaceae. Families containing Type II or III elements include Leguminosae, Elaeocarpaceae, Tiliaceae, Sapindaceae, Meliaceae, Compositae, Moraceae, Urticaceae, Casuarinaceae, Ulmaceae, Garryaceae, Sterculiaceae, and most of the sympetalous families. It should be noted, however, that some dicotyledonous families are very uniform in all genera and species as regards sieve tube element type, whereas other families are quite variable with elements ranging from Type I to Type III occurring in different species. In regard to this extreme variation in sieve element type, Esau (1969) has pointed out that the weakness of this sieve tube element classification lies in the inadequacy of the material surveyed.

Carlquist (1961) noted that there is much variation in the levels of evolutionary advancement in the xylem and phloem within the Compositae. I have encountered a similar lack of correlation in the monotypic urticalean family Barbeyaceae, the single species of which has only simple vessel perforation plates and Type I sieve tube elements (Dickison & Sweitzer, 1970), and in *Saurauia* (Actinidiaceae) which has exceedingly primitive vessel elements with sometimes over a hundred scalariform bars, but Type III sieve elements. Within the Dilleniaceae, *Schumacheria*, the genus with the most primitive wood structure, has very advanced sieve tube elements with simple, transverse sieve plates. It is well known that tissues evolve independently and at different rates. However, the reason for such vast discrepancies in levels of advancement in the vascular tissue needs explanation. Quite clearly, much more comparative information on the phloem needs to be obtained.

PRIMARY VASCULAR SYSTEM

The trends of specialization in the primary xylem of dicotyledons tend to parallel those of the secondary xylem elements (Bailey, 1944), although the trends show an evolutionary lag between both protoxylem and metaxylem, and metaxylem and secondary xylem. All available evidence indicates that vessels arose in woody plants first in the secondary xylem of the stem and then appeared in the metaxylem and protoxylem. Thus, the primary xylem is a reservoir of primitive characters. The presence of vessels in the protoxylem is interpreted as an indication of extreme structural specialization (Bailey, 1944).

As in dicots, the primary xylem vessels of monocotyledons probably originated more than once from scalariformly pitted tracheids (Cheadle, 1953 and

references). However, the phylogenetic sequence is different; vessels in monocotyledons first arose in the late metaxylem of roots, as evidenced from the fact that the most specialized vessel elements always occur in the root metaxylem, and only subsequently extended into the stem and leaf. Within any one organ, vessel element origin and specialization occur first in the late metaxylem and then progressively in the early metaxylem and protoxylem. The distribution of vessel elements in monocotyledonous families shows that they may be restricted within the plant body to the root, to the root and stem, or that they may occur in all parts. Cheadle & Uhl (1948) classified the vascular bundles of monocotyledons into six types based on the appearance of metaxylem elements in transverse section. Utilizing the occurrence of tracheids or the type of vessel-element perforation plate in the late metaxylem as criteria for specialization, they arranged the bundle types in a phylogenetic sequence. However, the fact that vascular bundle type can change rather dramatically in different regions of the same plant casts some doubt on the usefulness of this interpretation.

In the opinion of Bailey (1944) and Cheadle (1953) the independent origins and specializations of vessel elements in monocots and dicots indicate that if the angiosperms are considered to be monophyletic, the monocotyledons must have arisen from a vesselless woody dicotyledon. Cronquist (1968, 1969), however, does not accept the position that vessels evolved independently in monocots and dicots and, therefore, that monocots arose from a primitively vesselless ancestor. In his view, monocots had an aquatic origin (which profoundly influenced their evolutionary history) from dicotyledonous ancestors resembling the modern Nymphaeales. The aquatic habit resulted in the loss of a cambium that resulted in the reduction and loss of vessels. In keeping with this viewpoint, the Alismatiidae are considered a near-basal sidebranch of the Liliatae. Kosakai et al. (1970) reported the occurrence of primitive vessel elements in the primary xylem of roots of *Nelumbo* and seriously questioned the idea that monocots were derived from the Nymphaeaceae. These authors emphasized that the Butomaceae and Alismataceae have advanced vessel elements only in the root metaxylem. Accordingly, it is difficult for them to believe, in view of what is known of vessel evolution, that the putatively primitive Alismatiidae evolved advanced vessels in an aquatic environment yet gave rise to terrestrial monocots that had more primitive vessel elements in the metaxylem of their roots. The vessel story, according to them, favors the origin of the Alismatiidae from terrestrial forms and does not support an aquatic "ranalean" ancestry of the monocotyledons.

Bierhorst & Zamora (1965) following an extensive survey of 1,350 species of angiosperms in 165 families concluded that tracheary elements that mature later in the protoxylem-metaxylem sequence are ontogenetically derived from early maturing protoxylem elements with helical secondary walls by the deposition of additional secondary wall material (second-order framework) in the form of sheets, strands, or both, between the helices (first-order framework) of existing elements. Furthermore, elements in which the second-order framework is deposited synchronously, uniformly, and along the cell edges, are interpreted as primitive, as opposed to advanced elements in which the second-order framework is deposited nonsynchronously and is not restricted to cell edges. The phylo-

NODAL PATTERNS

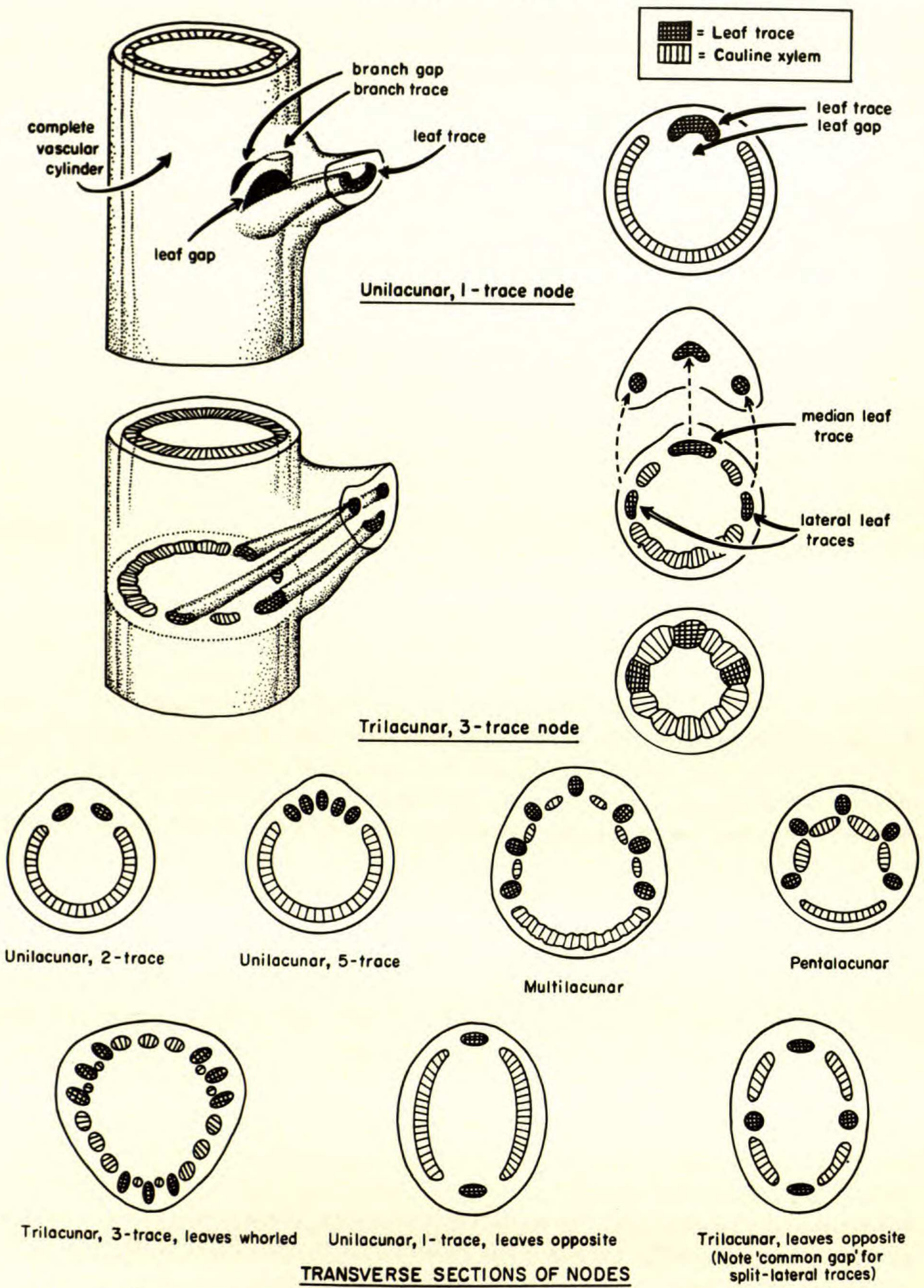


FIGURE 4. Variations in nodal structure in angiosperms. (From A. E. Radford, W. C. Dickison, J. R. Massey & C. R. Bell. Vascular Plant Systematics. Copyright 1974 by Harper & Row, Publ. Used with permission.)

genetic significance of these data, however, is unclear at the present time because the taxonomic distribution of primitive elements includes arborescent monocots (except Agavaceae), most Cyperaceae, Magnoliales, most woody amentiferous plants, Urticales, many woody Rosaceae and Saxifragaceae, and woody members of isolated families that are otherwise herbaceous.

NODAL ANATOMY

The node is that part of the stem to which leaves are attached. Nodal anatomy, accordingly, describes the pattern of vascular continuity between these two organs. Depending upon whether one, three, or five or more leaf gaps (i.e., parenchymatous interruptions) are left in the stele by the departure of vascular bundles (leaf traces) to the leaf, nodes are described as unilacunar, trilacunar, or multilacunar (Fig. 4). The nodal pattern is often expressed in terms of the number of traces and gaps, e.g., a unilacunar node with a single trace would be described as 1:1; a unilacunar node with two diverging traces would be 2:1; a trilacunar, three-trace node would be 3:3; and so on. The first figure represents the number of traces, the second figure the number of gaps in the vascular system of the stem.

Although most families tend to have a uniform nodal anatomy, some families and even genera have variable nodal structure. Trilacunar nodes occur in the majority of dicotyledons (Sinnott, 1914). Multilacunar nodes are relatively uncommon in dicotyledonous families (Howard, 1970), but are found in members of primitive orders such as Magnoliales, Piperales, and Trochodendrales, and advanced orders such as Umbellales and Asterales. The unilacunar node has an interesting distribution, namely, the Laurales (sensu Takhtajan), Caryophyllales, Ericales, Diapensiales, Ebenales, Primulales, Myrtales, and a majority of the families in the Asteridae. Some orders show transitions in nodal structure, e.g., the Theales from which Schofield (1968) described two possible lines of evolution originating from the ancestral trilacunar condition in the Dilleniaceae. One line maintained the trilacunar node, and eventual amplification culminated in the multilacunar node of the Caryocaraceae. The second line involved reduction to the unilacunar nodes of the Marcgraviaceae and Theaceae.

Since the first comprehensive study of nodal structure and evolution by Sinnott (1914), nodal anatomy has assumed much importance in discussions relating to angiosperm phylogeny. Whether the primitive nodal pattern was trilacunar (Sinnott, 1914), multilacunar (Ozenda, 1949), unilacunar, two-trace (Marsden & Bailey, 1955; Canright, 1955), or trilacunar or multilacunar with two traces diverging from the median gap (Takhtajan, 1969) has yet to be answered. The primary evidence used to support the primitive nature of the 2:1 node are its occurrence (or modifications thereof) in members of the Magnoliidae (Calycanthaceae, Lactoridaceae, Illiciaceae, Amborellaceae, Lauraceae, Chloranthaceae, Monimiaceae, Austrobaileyaceae, Schisandraceae, and Trimeniaceae), the distribution of this type in vascular plants other than angiosperms, and its presence in the cotyledonary node of many dicots even though the mature foliar nodes of the same plants may be tri- or multilacunar (i.e., cotyledonary nodes are conservative and thus reflect ancestral conditions).

Recent papers by Conde & Stone (1970) and Stone (1970) have described an amazing diversity of cotyledonary nodal patterns in the Juglandaceae in which nodal evolution appears correlated with functional demands of the seedling. These authors were able to confirm the 2:1 cotyledonary node as primitive in Juglandaceae and suggested the diversification to more complex patterns is functionally related to independent shifts within the family from epigeal to hypogeal seedlings. Furthermore, a suggestion was made that the apparent conservatism of cotyledonary nodes in dicotyledons as a whole may be directly related to the prevalence in many groups of primitive, epigeal germination. Cotyledonary nodal anatomy should, thus, be considered independently of the mature foliar nodes.

Namboodiri & Beck (1968) have recently proposed that the eustele of gymnosperms evolved directly from a protostele by gradual medullation and longitudinal dissection, followed by formation of a cylinder of longitudinal sympodial bundles from which leaf traces diverge radially. In this interpretation the primary vascular system of seed plants is not directly comparable to that of ferns so that the classic filicinean-type leaf gaps may not occur in eusteles. This concept has also been extended to angiosperms (Slade, 1971; Devadas & Beck, 1972). Benzing (1967) concluded that the unilacunar, one-trace or trilacunar, three-trace nodal pattern was probably primitive and agrees with previous workers that the magnolialian families with 2:1 nodes are distinguished by rather advanced floral characters and a presumably derived decussate phyllotaxy.

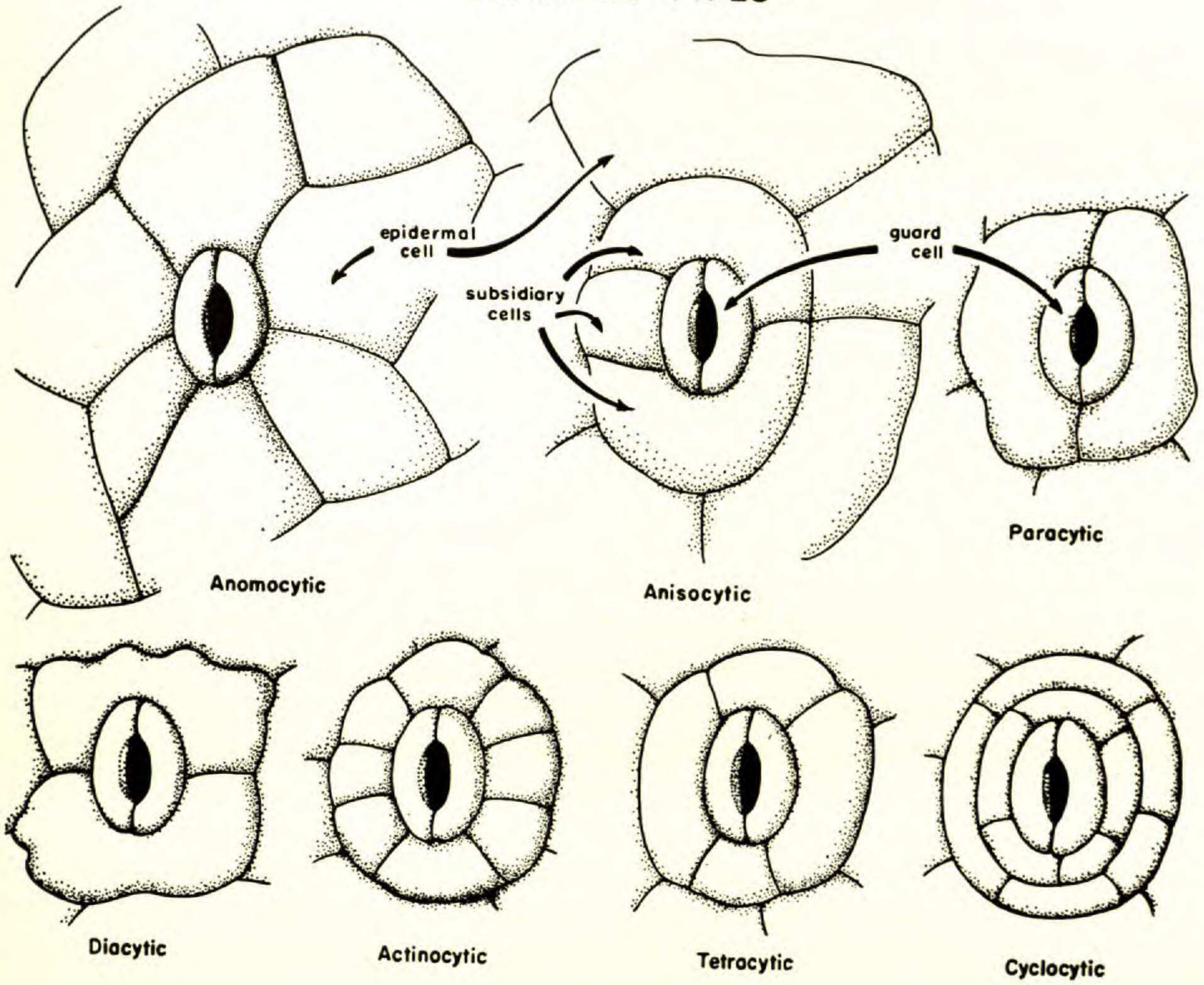
Howard's (1970) account of nodes with "split-lateral" traces further emphasizes our incomplete knowledge of nodal structure and evolution. Correlating data dealing exclusively with primary vascular systems and studies of nodes in which secondary growth has occurred has yet to be done. Howard (1970) also points out the need for detailed descriptions of nodal vasculature in which the size of bundles, type of bundles, course of bundles, and role of cortical and medullary bundles is taken into account. The entire subject of the stem-node-leaf continuum has been the subject of a recent extensive review by Howard (1974). This paper includes descriptions, methods of study, and discussions of the systematic and evolutionary value of information from this part of the plant body.

LEAVES

Carlquist (1961) has stated that the leaf is "perhaps anatomically the most varied organ of angiosperms, and its anatomical variations often concur closely with generic and specific, occasionally familial, lines." Although anatomical leaf characters are generally useful in the delimitation of taxa, the majority of these characters cannot be readily interpreted ecologically or evolutionally. For example, in the genus *Cratoxylum*, Baas (1970) found the presence or absence of epidermal papillae and a hypodermis able to vary enormously within one subspecies without any evident ecological reason. A few of the characters of leaf anatomy that have proven to be of systematic value and are of potential phylogenetic significance are the following:

Cuticle.—Cuticular features include such characters as distribution and orientation of papillae, striae, and rods.

STOMATAL TYPES



SCLEREID TYPES

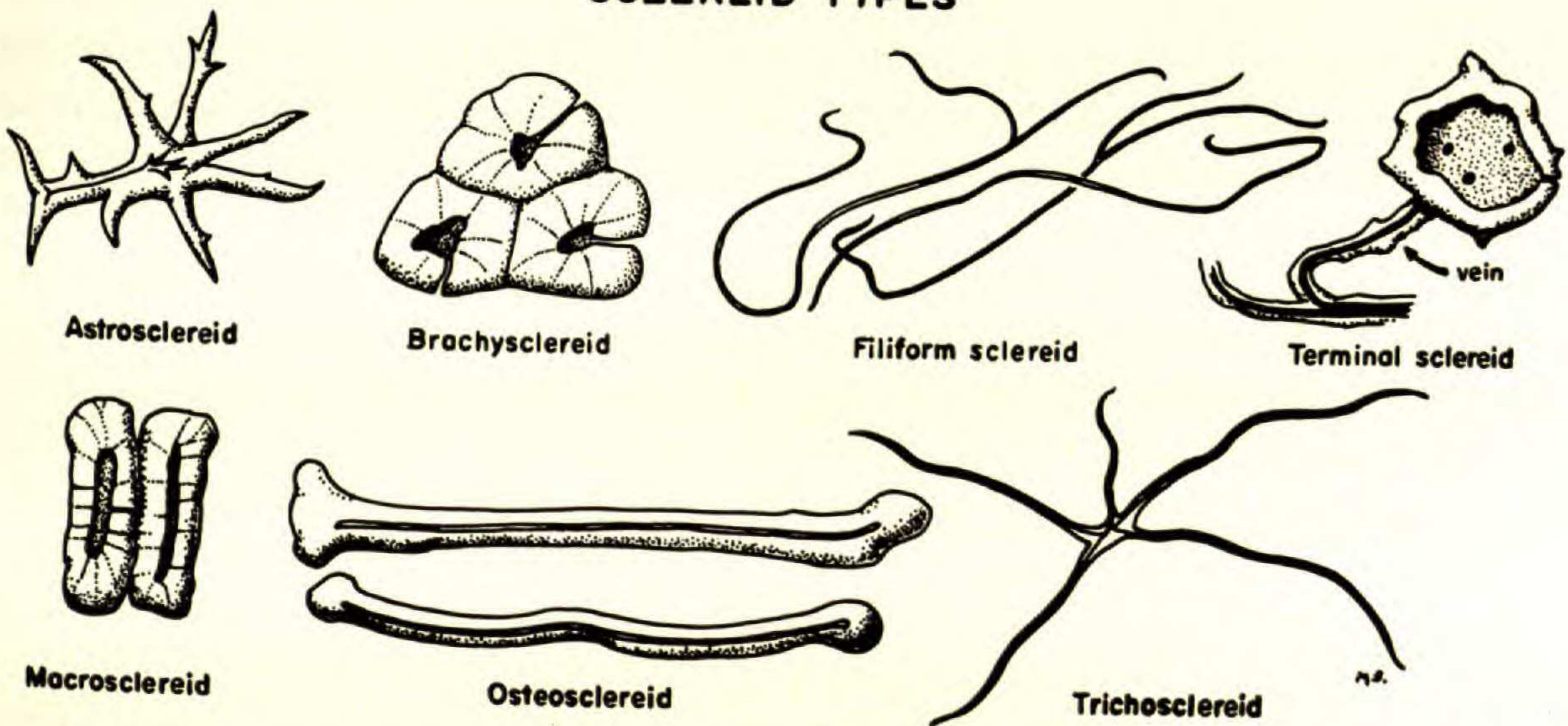


FIGURE 5. Mature stomatal and sclereid types in angiosperms. (From A. E. Radford, W. C. Dickison, J. R. Massey & C. R. Bell. *Vascular Plant Systematics*. Copyright 1974 by Harper & Row, Publ. Used with permission.)

Epidermis.—Epidermal characters of importance are the presence of a uniseriate or multiseriate epidermis, thickness of walls, and size, shape and contents of cells including the occurrence of papillae and mucilage. Although trichomes have been classically employed for systematic purposes, a classification has yet to be proposed which satisfactorily accounts for their morphological diversity. Metcalfe & Chalk (1950) in commenting upon plant hairs state that “the various types are not always clearly defined, however, and their value for systematic purposes is lessened by the fact that many kinds occur in families which are generally thought to be unrelated, thus making it reasonably certain that the same type of hair must have been evolved along independent lines.” Phylogenetic trends in trichomes for angiosperms as a whole have been suggested (see Carlquist, 1961) but they have not had significant influence on phylogenetic thought.

Diversity of stomatal types offers one of the most important and readily observable epidermal characters. Stomatal classification is based, for the most part, on the relationship of subsidiary cells (i.e., epidermal cells associated with a stoma and morphologically distinguishable from the epidermal cells composing the ground mass of the tissue) to remaining epidermal cells and guard cells. The following types of angiosperm stomata are based on their mature appearance (Fig. 5). Definitions follow van Cotthem (1970). (1) Anomocytic (irregular-celled, ranunculaceous type), stoma surrounded by a limited number of cells that are indistinguishable in size, shape, or form from those of the remainder of the epidermis; (2) Anisocytic (unequal-celled, cruciferous type), stoma surrounded by three cells of which one is distinctly smaller than the other two; (3) Paracytic (parallel-celled, rubiaceus type), stoma accompanied on either side by one or more subsidiary cells parallel to the long axis of the pore and guard cells; (4) Diacytic (cross-celled, caryophyllaceous type), stoma enclosed by a pair of subsidiary cells whose common wall is at right angles to the guard cells; (5) Tetracytic, four subsidiary cells are present, two lateral and two terminal; (6) Actinocytic, stoma surrounded by a circle of radially elongated subsidiary cells which form a ring around each stoma; (7) Cyclocytic, stoma surrounded by four or more subsidiary cells which form a ring around each stoma; and (8) Hexacytic, stoma accompanied by six subsidiary cells consisting of two lateral pairs parallel to the long axis of the pore and two polar (terminal) cells; the second lateral pair are as long as the stomatal complex. (This type could be described as a modification of the tetracytic type with an additional pair of lateral subsidiary cells.)

Trends of evolution among stomata types have long been unclear. On the basis of the nearly uniform occurrence of paracytic stomata in the Magnoliales (sensu Takhtajan), Baranova (1972) has recently advocated paracytic types as primitive within the angiosperms. The only taxa in the order lacking this stomatal pattern are *Liriodendron tulipifera* (Magnoliaceae) and *Bubbia perrieri* (Winteraceae), both advanced in their respective families. Correlated with paracytic stoma in the Magnoliales are thickened lamellae on the outer walls of the guard cells and thick-walled epidermal cells with pores in the outer wall, both characters regarded by Baranova (1972) as primitive in angiosperms as a whole. Since it is well known that similar mature stomatal patterns can arise by different developmental path-

ways, an extension of this work utilizing the ontogenetic classification of stomata types by Fryns-Claessens & van Cotthem (1973) would be desirable. It should be noted that paracytic stoma are found in a large number of unrelated and often advanced families. Tomlinson (1974) observes that there are no major groups of monocotyledonous families characterized by a specific type of stomatal development and that speculations regarding the phylogenetic significance of stomatal patterns are premature.

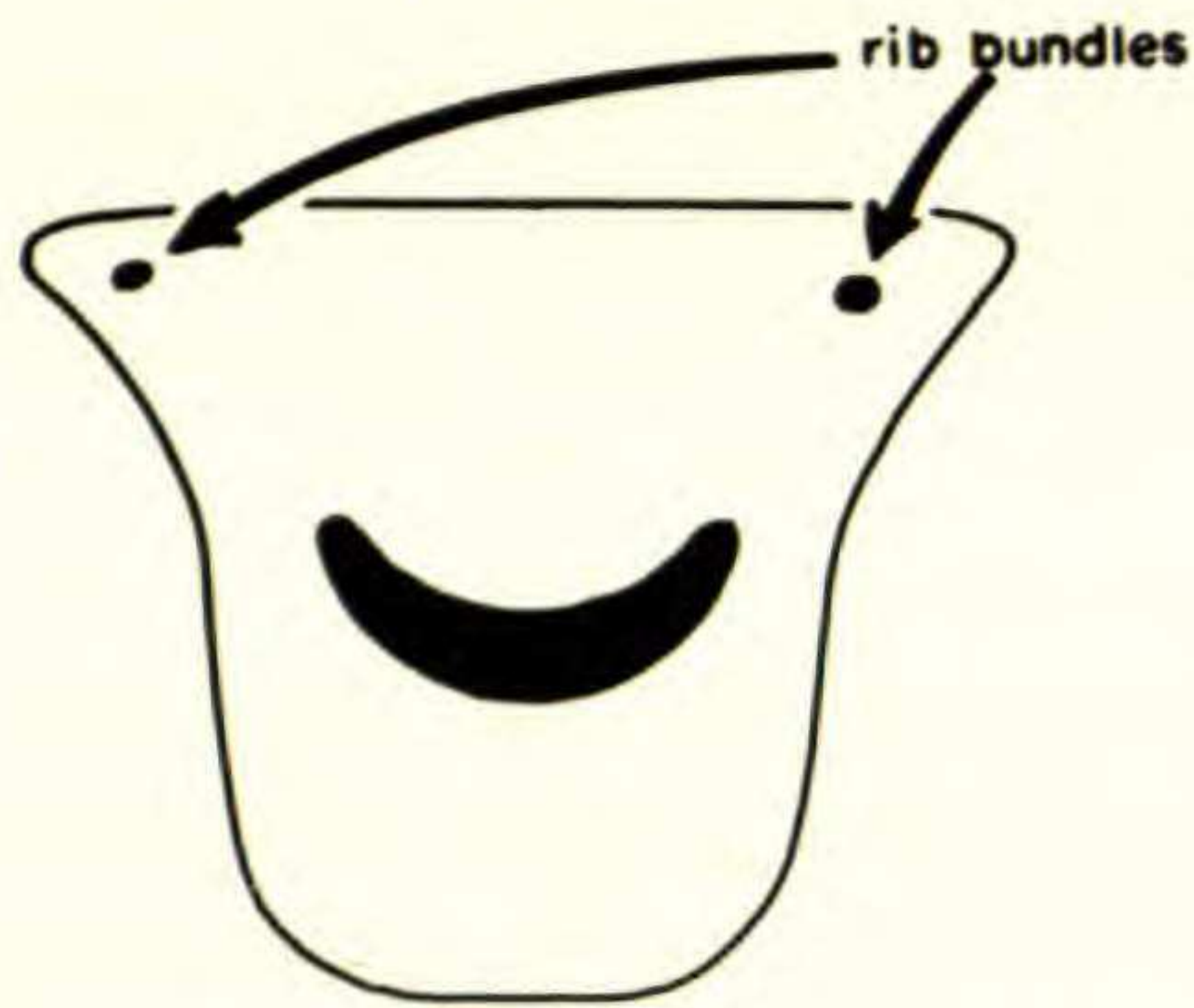
Mesophyll.—Characters of the mesophyll of taxonomic value include the types of mesophyll (bifacial or isolateral) and features of construction, such as relative differentiation into palisade and spongy layers and number of layers in each, distribution and shape of mesophyll cells (isodiametric, stellate, thick-walled), and presence or absence of air-lacunae. The presence or absence of a hypodermis, i.e., a layer or layers of cells beneath the epidermis (either adaxial or abaxial) morphologically distinct from underlying layers, and the number of layers of hypodermal cells are often diagnostic. Also, the presence, absence, and distribution of secretory canals and crystals are frequently of systematic value.

Sclerenchyma.—Leaf sclerenchyma is of two types, sclereids and fibers. A sclereid is a cell varied in form but typically not much elongated, and having thick, lignified secondary walls with many pits. A fiber is an elongated, tapering sclerenchyma cell with a more or less thick secondary wall. Types of sclereids (Fig. 5) based on form include: (1) astrosclereids, branched (ramified) types of sclereid; (2) brachysclereids (stone cells), short, roughly isodiametric sclereids resembling parenchyma cells in shape; (3) filiform sclereids, much elongated and slender, resembling fibers; (4) macrosclereids, somewhat elongated with unevenly distributed secondary walls; (5) osteosclereids, "bone-shaped," with columnar middle part and enlargements at both ends; and (6) trichosclereids, branched, with thin hairlike branches extending into intercellular spaces. Sclereid types based on distribution are (1) diffuse sclereids which are dispersed in the leaf mesophyll, and (2) terminal sclereids which are confined to the ends of small veins. Leaf fibers are termed: (1) girders (a sclerenchymatous connection between a vascular bundle and the epidermis); (2) incomplete (partial) girders (a sclerenchymatous extension from the bundle sheath which does not reach the epidermis); and (3) strands (sclerenchyma free from the vascular bundle sheath and which may be subepidermal). The occurrence and taxonomic usefulness of foliar sclerenchyma in widely diverse families of flowering plants has been well established. Bokhari & Burt (1970) reported an extraordinarily diverse sclereid composition in the genus *Cyrtandra* (Gesneriaceae) and correlated sclereid morphology with tentative groupings of species made from morphological considerations. Trends of evolution of leaf fiber patterns have been suggested by Ayensu (1973) in the Velloziaceae. In the Magnoliaceae, Tucker (1964) has described apparent phylogenetic trends of specialization among the terminal idioblasts, viz., one toward tracheary cell types, one toward sclerenchymatous terminal cells, and a third toward parenchymatous terminal cells. Since specialized terminal cells are rather widespread in dicotyledons, this character has potentially wider phylogenetic significance.

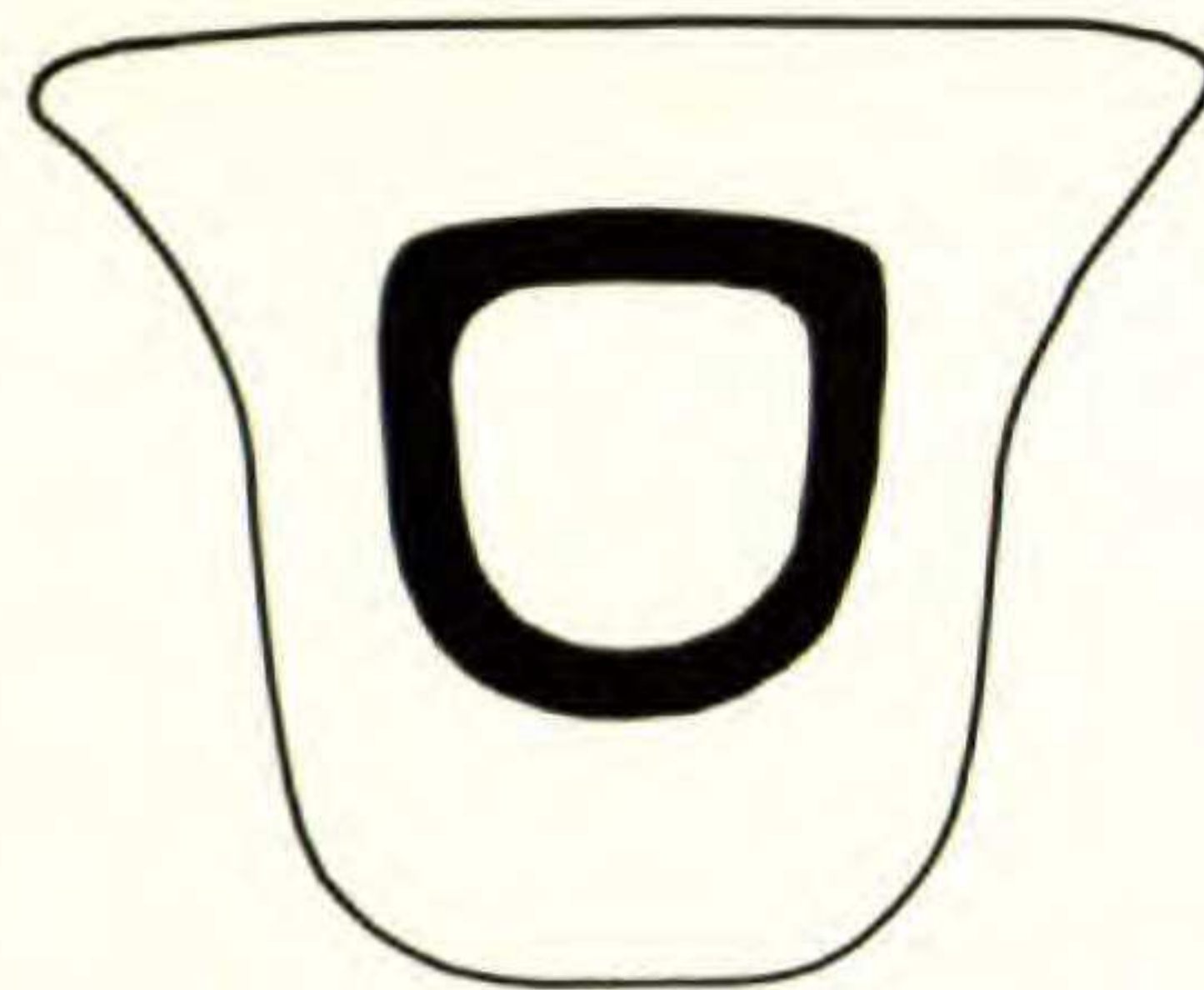
Venation.—The taxonomic and phylogenetic usefulness of leaf venation pat-

COMMON PETIOLE VASCULATION PATTERNS

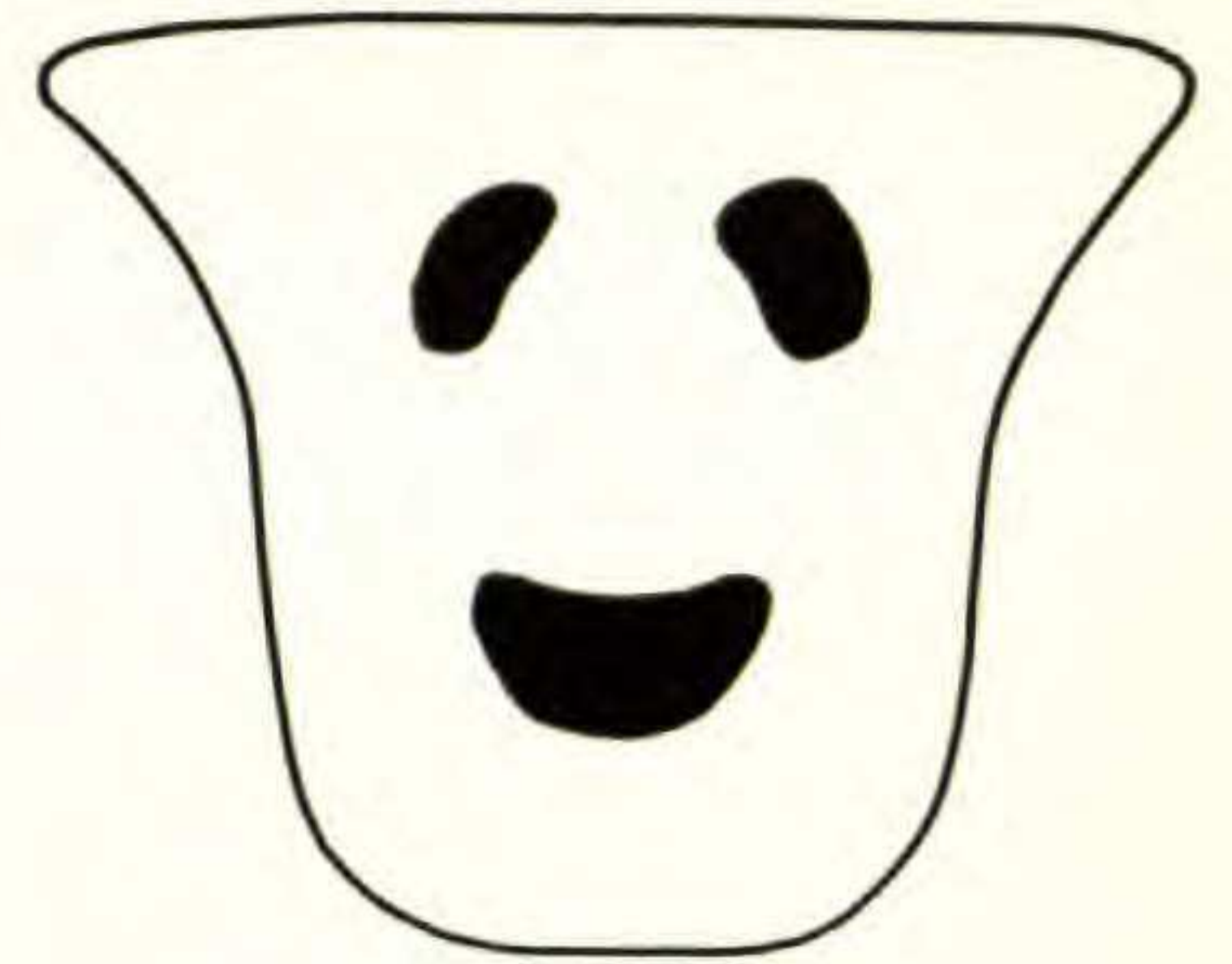
(Transverse Sections at Base of Lamina)



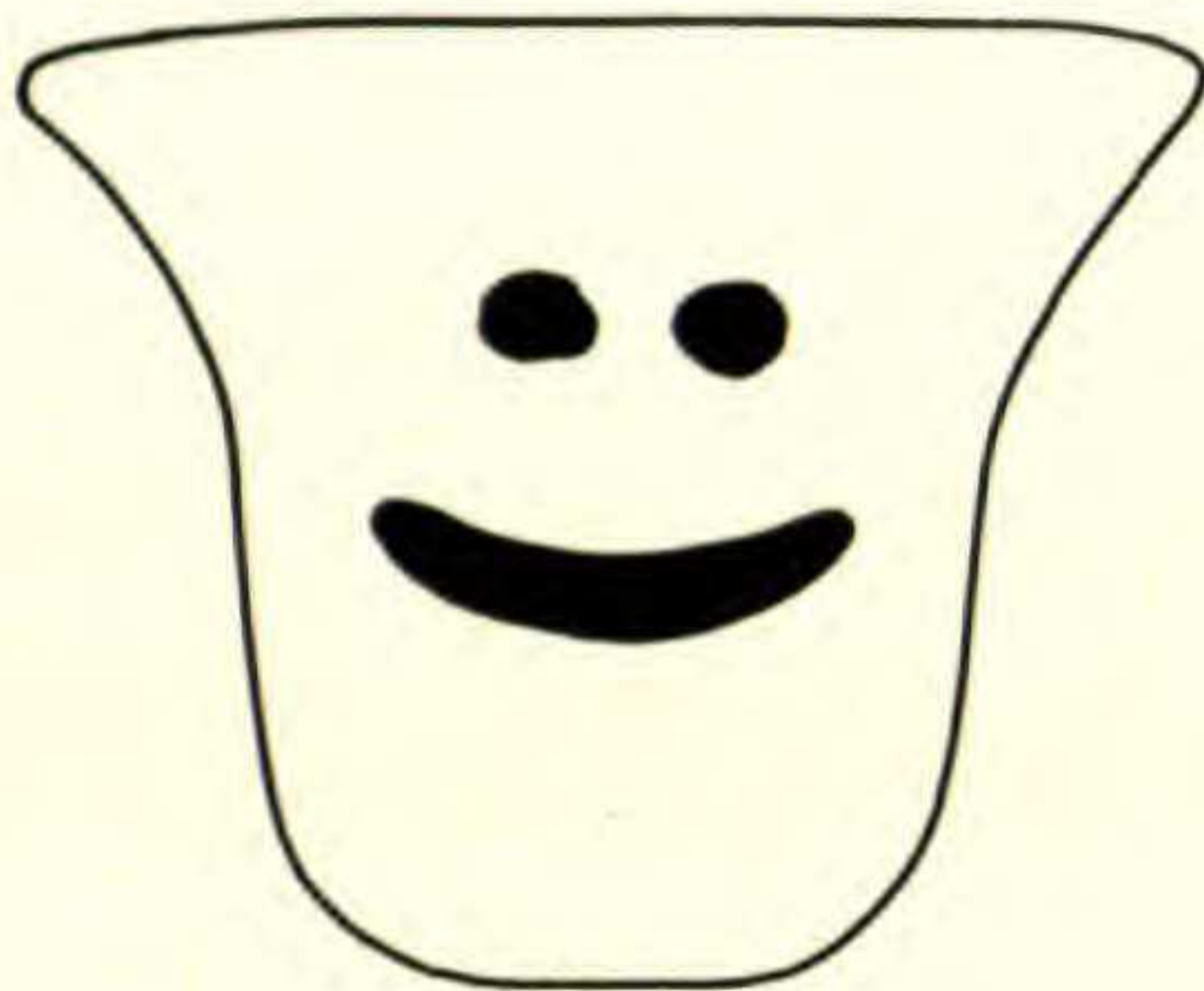
Flat arc with rib traces



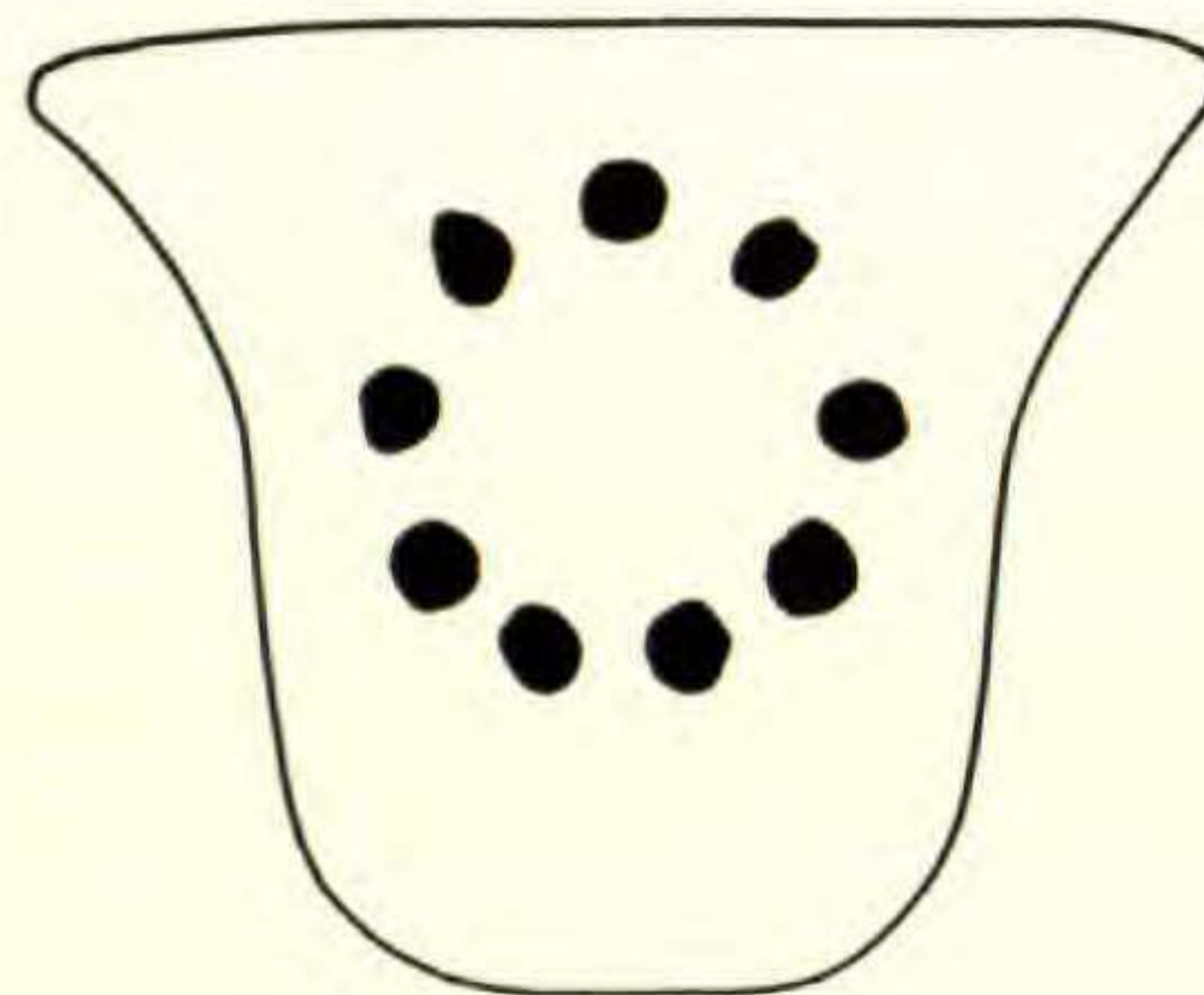
Medullated vascular cylinder



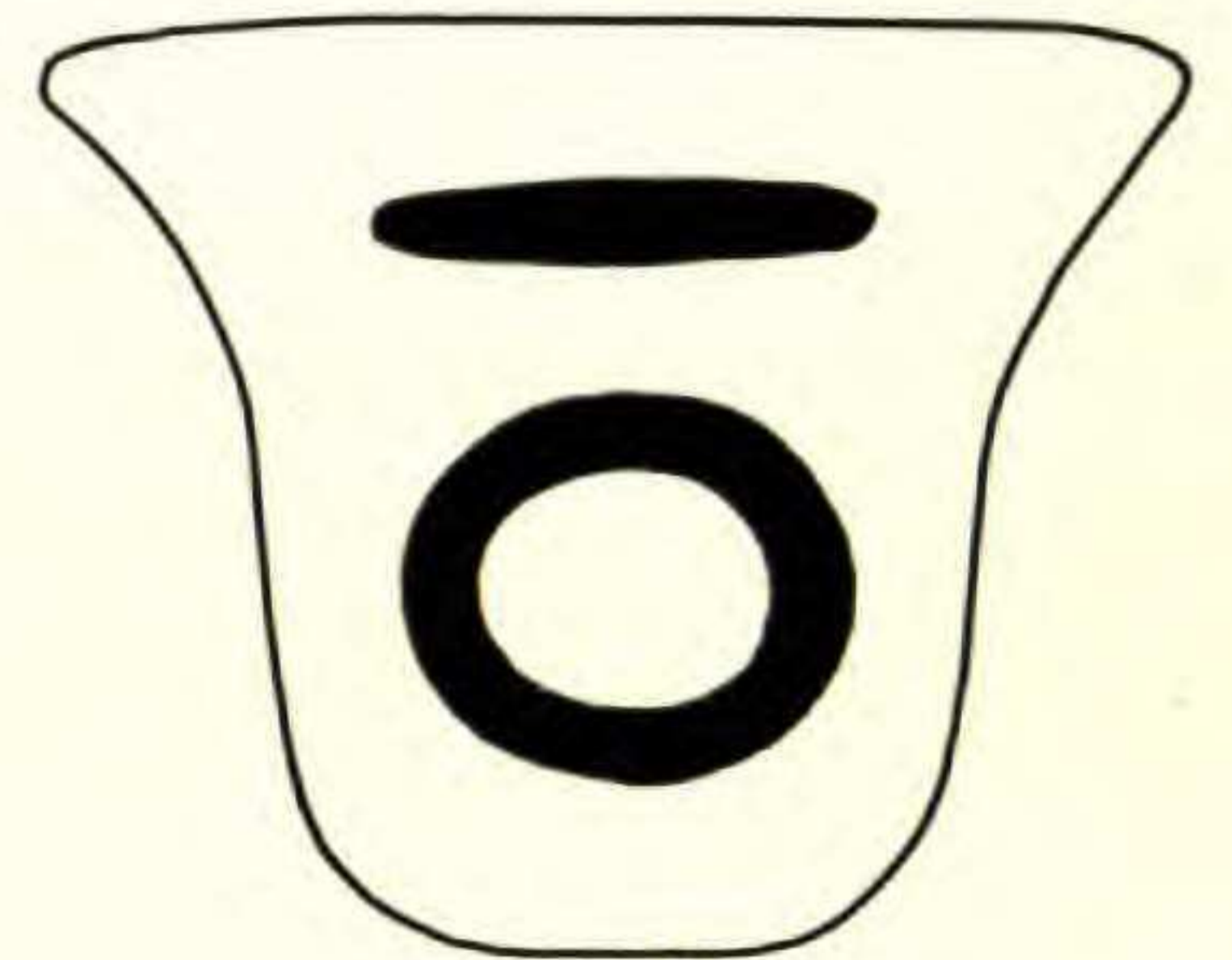
3 Free traces



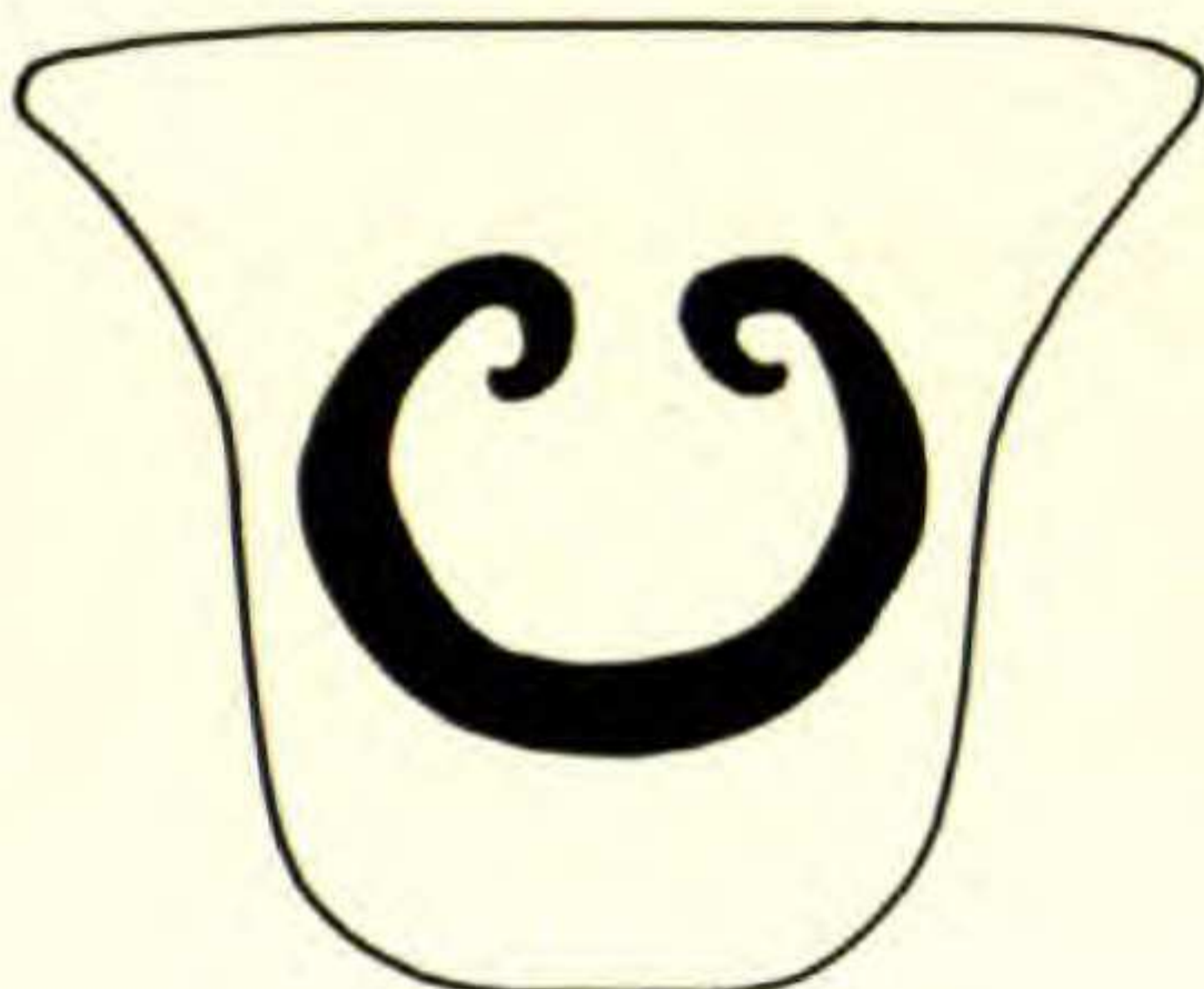
Flat arc with dorsal traces



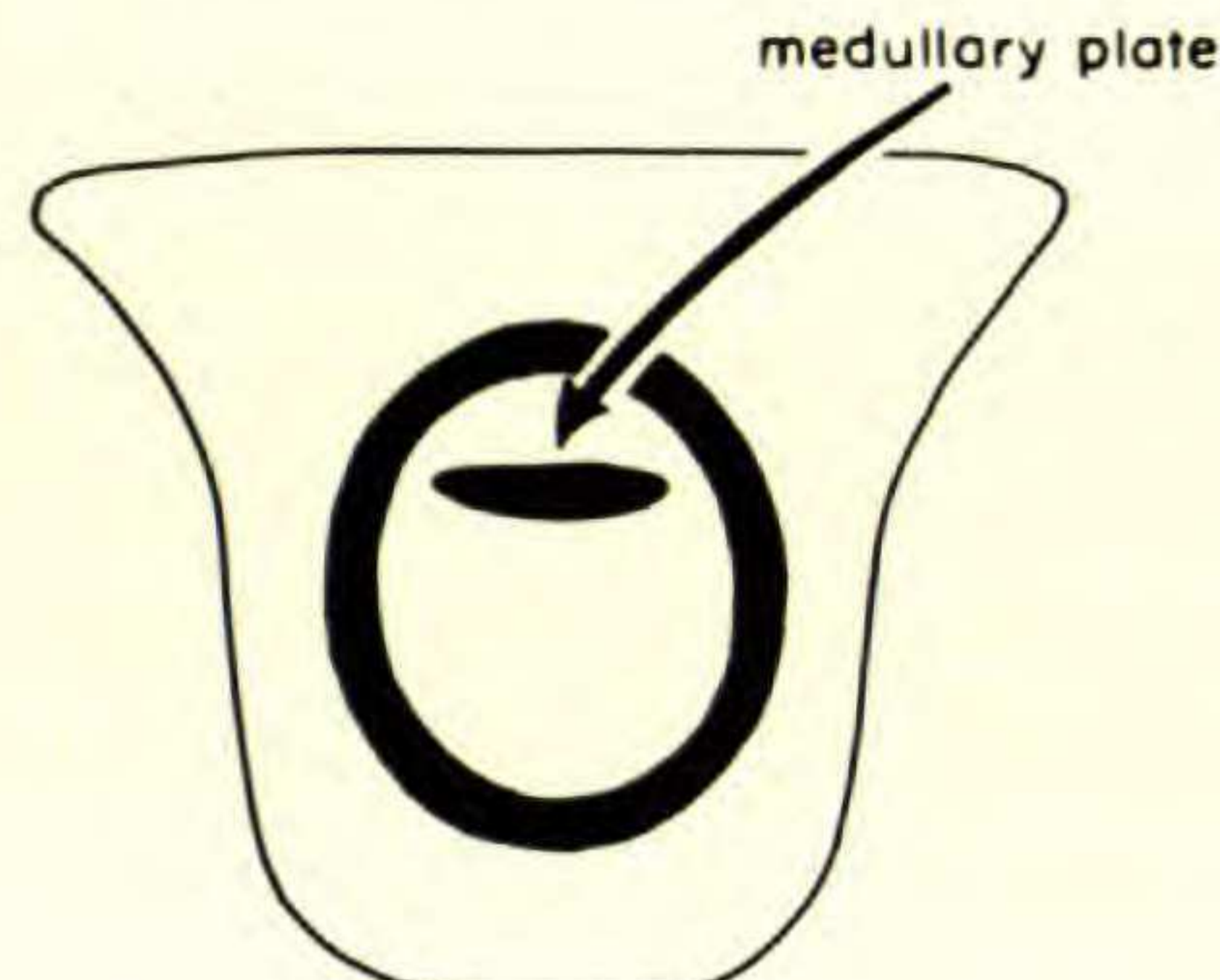
Many free traces in ring



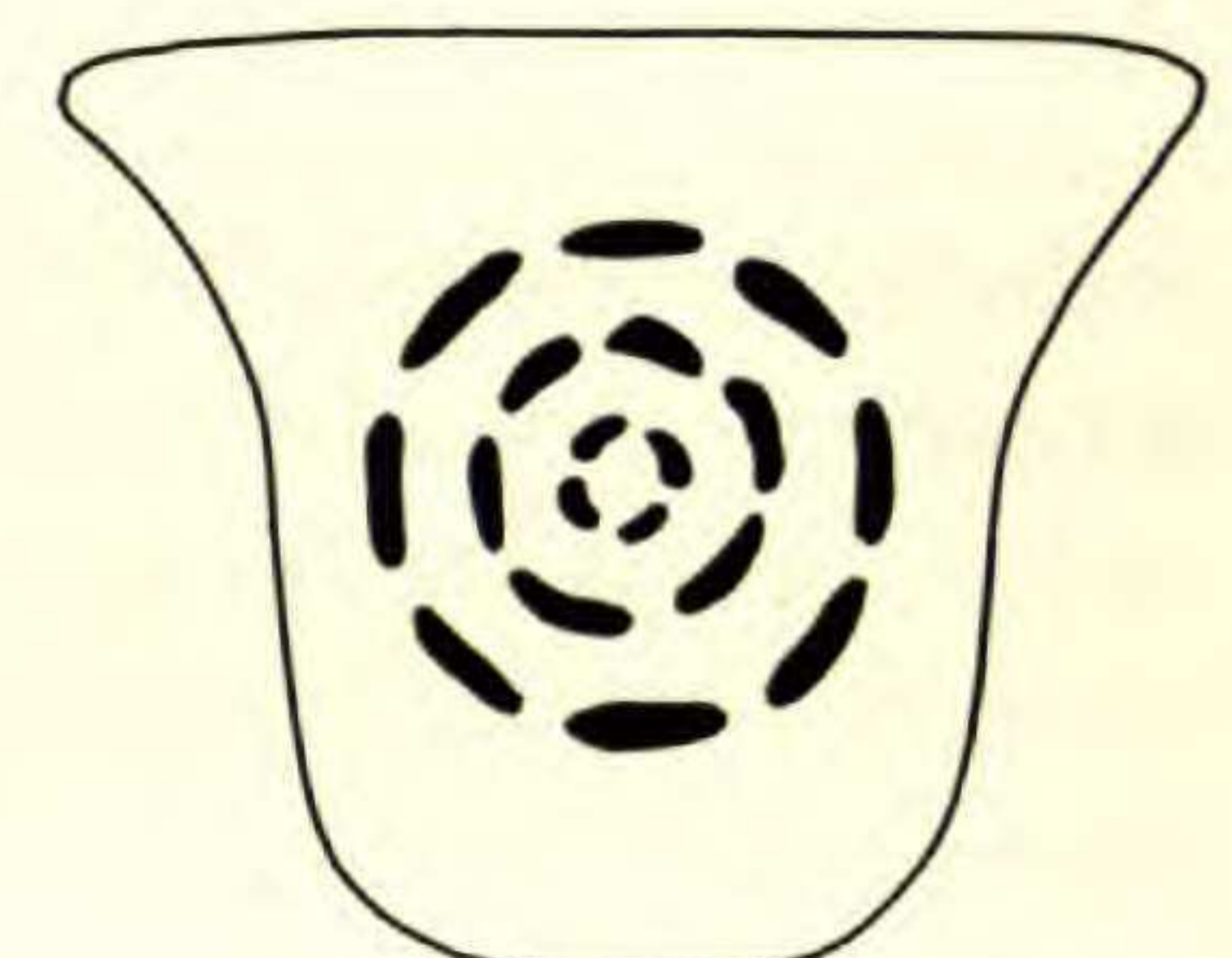
Medullated cylinder with dorsal plate



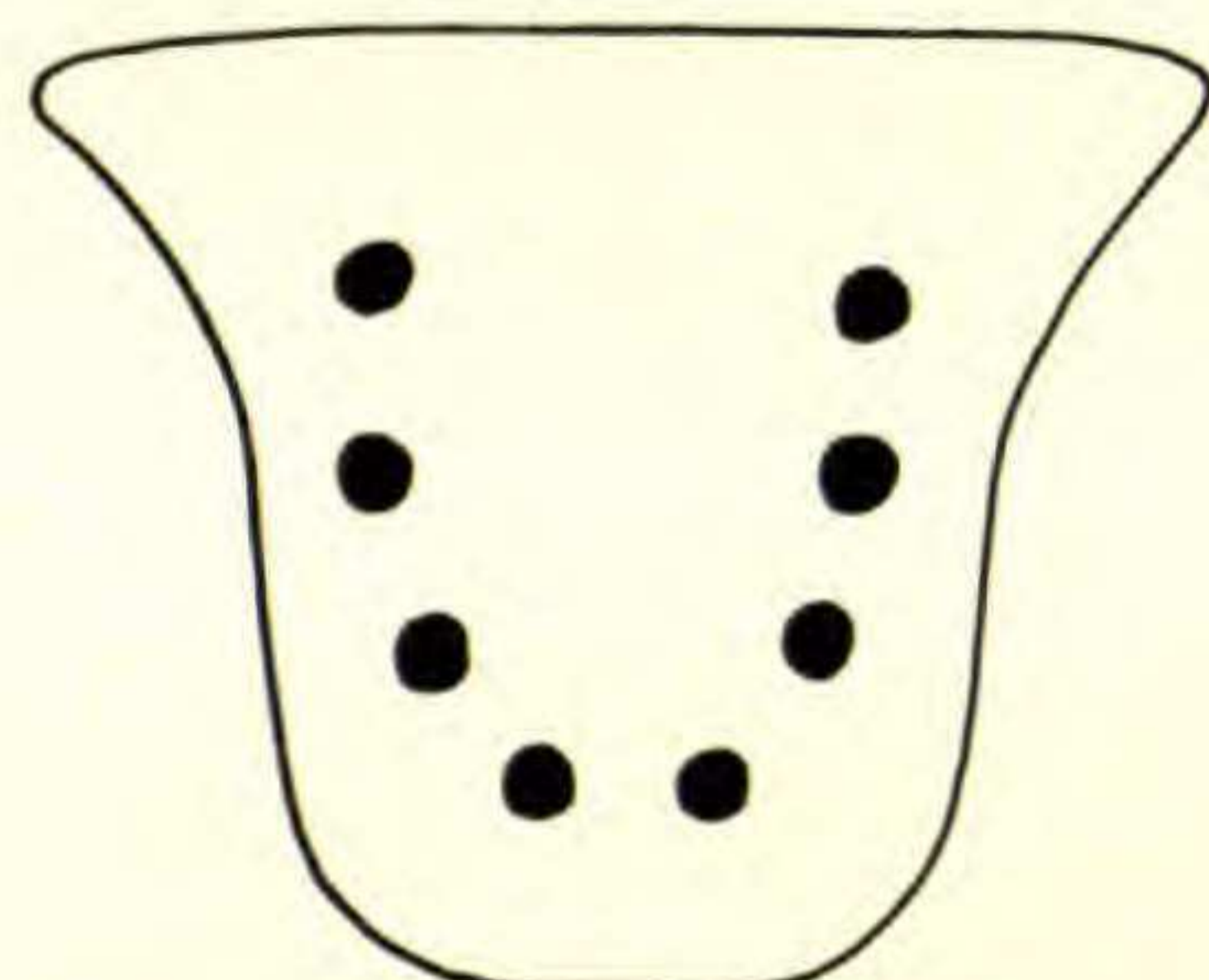
Arc with invaginated ends



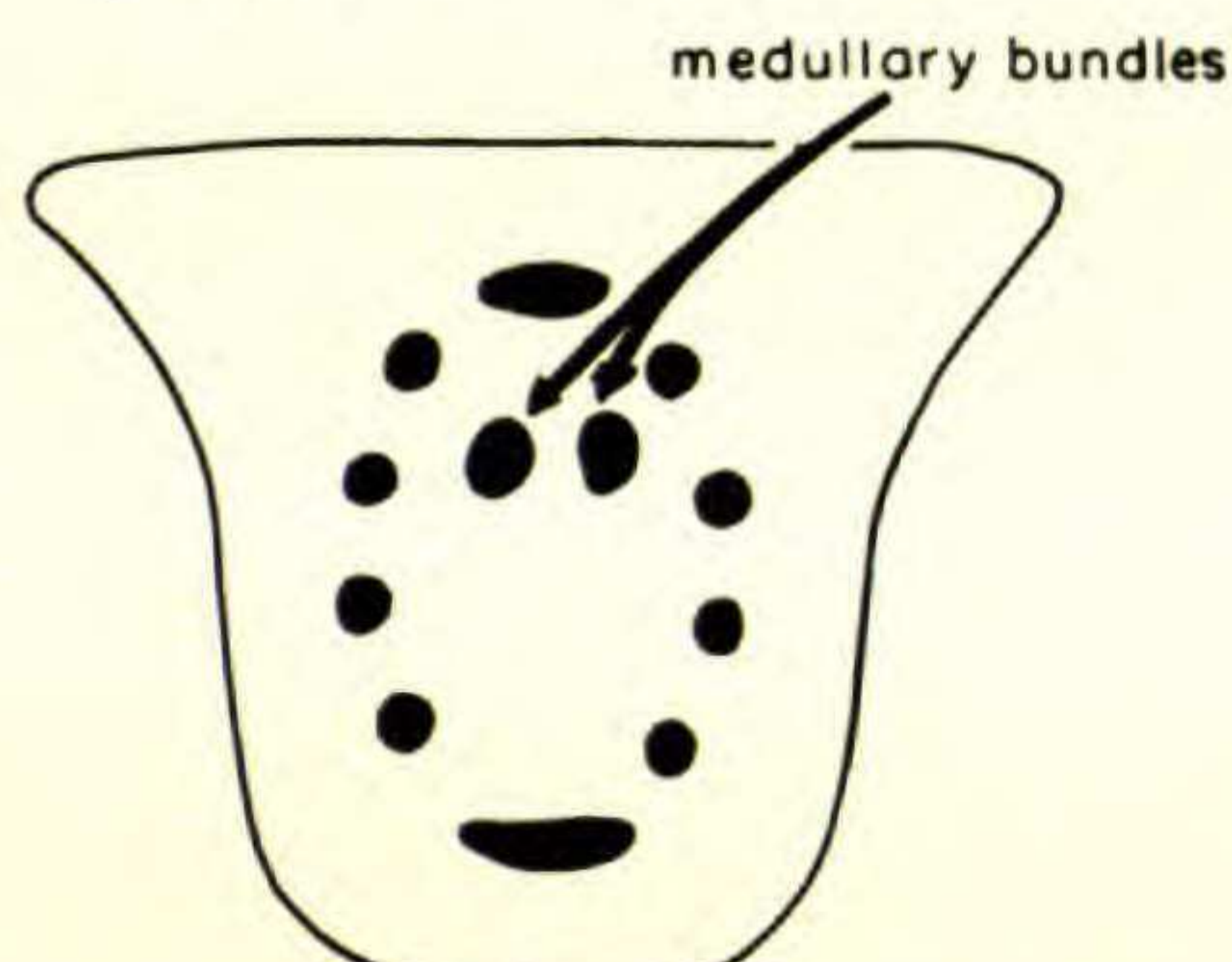
Medullated cylinder with medullary plate



Free traces in concentric rings



"U"-shaped free bundles



Many free traces in ring with medullary bundles



Open medullated cylinder with lateral rib traces

FIGURE 6. Common petiole vascularization patterns in wood dicotyledons. (From A. E. Radford, W. C. Dickison, J. R. Massey & C. R. Bell. *Vascular Plant Systematics*. Copyright 1974 by Harper & Row, Publ. Used with permission.)

terns has become increasingly apparent in recent years (see Hickey & Wolfe, this symposium). In addition to patterns of major and high order venation, the nature of vein sheathing should also be studied. Sheathing, if present, can be parenchymatous, sclerenchymatous, or a combination of both types to form double sheaths.

The most complete system of classification of major venation patterns in the petiole of woody dicotyledons (Fig. 6) is that of Howard (1962, 1974) although Dr. William L. Stern (personal communication) has questioned the use of stelar terminology in this context. Howard's classification emphasizes the importance of examining sections throughout the length of the petiole to completely understand the changes that occur in the vascular configuration. Accordingly, consideration is given to changes that occur in the vascular system from the time it leaves the stem until it becomes relatively stable in the leaf, e.g., arrangement of the vascular tissue (separate or fused bundles, scattered bundles, medullary bundles, etc.), outline of the vascular tissue (flattened, crescent-shaped, circular, etc.), and location and abundance of sclerenchyma.

Although there is considerable anatomical diversity in petiolar vascularization, trends of evolution in this region of the plant are not readily discernible in angiosperms as a whole. I see little or no obvious correlation between nodal anatomy type and petiole vascularization patterns. Suggested trends of specialization within specific families have been in conflict. For example, within the Dilleniaceae I regarded trilacunar nodes and petioles with unfused bundles more primitive than multilacunar nodes and conditions of fused petiole vascular bundles and the formation of more complex patterns with medullary bundles (Dickison, 1969). These ideas of nodal and petiolar evolution in Dilleniaceae did not agree with the conclusions of Decker (1967) who worked on the Luxemburgieae (Ochnaceae). Within the Luxemburgieae, Decker considered the multilacunar node more primitive than the trilacunar, and petioles with numerous unfused bundles (some of which may be medullary), more primitive than petioles with fused traces and no medullary bundles. In view of the frequent derivation of the Ochnaceae from the Dilleniaceae such contrasting opinions are of interest. Nevertheless, as trends of evolution in laminar venation become clarified and correlated with the petiole in reference to the functional demands of petiole vasculature, then the value of petiole vascularization data for the interpretation of angiosperm phylogeny will increase.

SUMMARY AND CONCLUSIONS

One of the major contributions of the Cronquist and Takhtajan systems of angiosperm classification was the creation and arrangement of rather large subclasses that reflect major levels of evolution in the angiosperms. Anatomical evidence, in a general way, correlates with evidence elsewhere in the plant to support an arrangement in which the Magnoliidae are the most primitive subclass from which the other angiosperm groups have been derived. The phylogeny of the monocots is much less clear and anatomical studies have yet to provide substantial support to any one idea. Some of the primary contributions anatomy can provide

in the future are to assist in the delimitation of orders and realignment of families and genera, and to help systematically place "anomalous" taxa.

A point stressed in the present paper is that whereas some vegetative anatomical characters can be interpreted as "major trends" of evolution in angiosperms, other anatomical features are only general or diagnostic characters that have no apparent phylogenetic value but may lend support to ideas formulated on other bases. Vegetative anatomical characters whose phylogenetic potential have yet to be fully evaluated and synthesized include aspects of seedling anatomy, origin and anatomy of the periderm, nature of the fundamental tissue and idioblastic cells, and developmental studies of the shoot apex (see Gifford, 1954) and other plant parts. Recent studies on leaf growth and differentiation by Kaplan (1970a, 1970b) have suggested that there is a common pattern of foliar development even among leaves of strikingly different mature form. Evidence of this type has obvious important implications in the solution of problems of plant phylogeny. Because there is a paucity of comparative information on roots, any phylogenetic conclusions based on this organ are premature. With new information being uncovered and correlated with already existing data, new trends of structural evolution in flowering plants are emerging, and trends that were once believed to be well-founded are now being seriously questioned. Clearly, secondary xylem has provided the most useful information toward solving problems of angiosperm phylogeny. This has largely resulted because successful methodologies were employed in studying this tissue. The tremendous wealth of anatomical evidence available in other tissues of the vegetative plant body will likewise become of immeasurable value to phylogeny when techniques are found to provide more meaningful phylogenetic interpretations of these data. For this to be realized, comprehensive anatomical studies need to be carried out utilizing a wide range of materials and approaches that integrate comparative data with development, functional demands of the plant, environmental variation, and the possible adaptive significance of the characters concerned. It may come as a surprise to some to learn that a vast amount of basic descriptive information has yet to be gathered, particularly applying precisely defined terms in current usage. Until a better understanding of the trends of evolution within specific families and genera are attained, there is less hope of uncovering major lines of anatomical specialization within angiosperms as a whole.

The more significant guiding principles of systematic anatomical study as related to angiosperm phylogeny have been eloquently discussed by I. W. Bailey (1951, 1953, 1957). Anatomical characters are no more or less reliable than characters from other parts of the plant. Evolutionary modification of vegetative anatomical characteristics are not necessarily closely synchronized with floral evolution. Since similar anatomical structures have arisen many times in widely divergent taxa, similarities in structural specialization do not necessarily imply close relationship but may be the result of parallel and convergent evolution. As a result, anatomical data have proven most reliable in statements of negation of close relationship rather than positive assertions of relationship. Only when anatomical information is coupled with evidence from other parts of the plant, will a phylogenetic classification of angiosperms be attained.

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